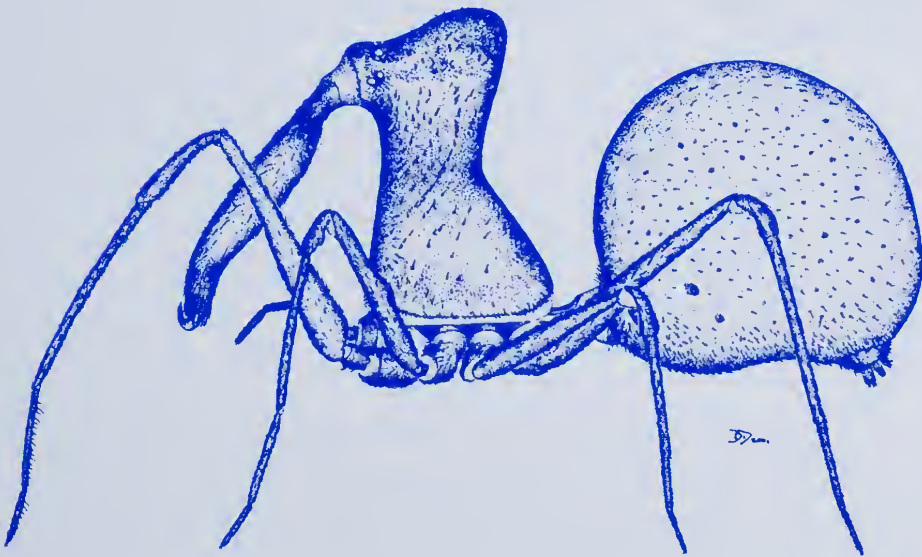


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Cover: *Austrarchaea robinsi*, a new species of spider from Western Australia.

Illustration by Bradley Durrant.



Two new species of *Ainudrilus* (Clitellata: Tubificidae) from south-western Australia, with notes on *Ainudrilus nharna* Pinder and Brinkhurst

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Abstract – Two new species of *Ainudrilus* are described from south-western Australia and the description of *A. nharna* is amended. *Ainudrilus angustivasa* sp. nov., from Lake Logue near Eneabba, is characterised by simple spermathecal ducts, thin vasa deferentia and lack of hair chaetae. *Ainudrilus ngopitchup* sp. nov., from a swamp near Kojonup, has long spermathecal ducts, broad vasa deferentia and hair chaetae.

INTRODUCTION

The freshwater representatives of the tubificid genus *Ainudrilus* were recently reviewed by Pinder and Brinkhurst (2000). Four freshwater species, all from Australia and numerous marine species, from Australia and elsewhere in the Pacific and Caribbean, are currently recognised (Erséus, 1990, 1997; Finogenova, 1982). Two new species have recently been collected from freshwater wetlands sampled during a biological survey of the wheatbelt and adjacent coastal areas of south-western Australia. Wetlands in this region are threatened by secondary salinisation and waterlogging resulting from rising groundwater caused by replacement of perennial native vegetation by annual crops that use less water (George *et al.*, 1995). The biological survey is designed to provide a framework for planning the conservation of regional biodiversity in the face of this threat. Non-marine tubificids are particularly sensitive to salinity and discovery of two new species in the south-west, which otherwise has only one endemic tubificid (*Ainudrilus nharna* Pinder and Brinkhurst, 2000), is of conservation significance in relation to the above environmental concerns.

MATERIALS AND METHODS

The two new species were collected in samples of benthic invertebrates taken using a D-frame sweep net with a mesh pore size of 250 µm and preserved in ethanol. Specimens were stained with Grenacher's borax carmine, cleared with methyl salicylate and slide mounted in Permount®, either whole or with the genital segments dissected. Type material is deposited with the Western Australian Museum (WAM) with other material held by the Department of Conservation and Land Management (CALM).

SYSTEMATICS

Subfamily Rhyacodrilinae

Genus *Ainudrilus* Finogenova, 1982

Type species

Ainudrilus oceanicus Finogenova, 1982 by original designation.

Diagnosis

Hair chaetae present or absent. Chaetae of penial segment modified, chaetae of spermathecal segment usually unmodified. Vasa deferentia usually broad and glandular, entering atria medially to subapically. Atria variably shaped but usually more or less erect or directed posteriad, consisting of an ampulla, often constricted medially and with spacious lumen, often containing sperm, usually leading to well developed ejaculatory ducts. Prostate absent. Penes absent, though ejaculatory ducts often eversible. Spermathecae with distinct, and often complex ducts. Sperm loose in spermathecal ampullae. Coelomocytes large and generally abundant.

Included Australian freshwater species: *Ainudrilus fultoni* (Brinkhurst, 1982), *A. billabongus* (Brinkhurst, 1984), *A. stagnalis* Erséus, 1997, *A. nharna* Pinder and Brinkhurst, 2000, *A. angustivasa* sp. nov. and *A. ngopitchup* sp. nov.

Ainudrilus nharna Pinder and Brinkhurst, 2000 Figure 1

Ainudrilus nharna Pinder and Brinkhurst, 2000: 55,
Figure 3.

Material examined

Holotype and Paratypes

Frankland River at Roe Road ford, 34 km NNW

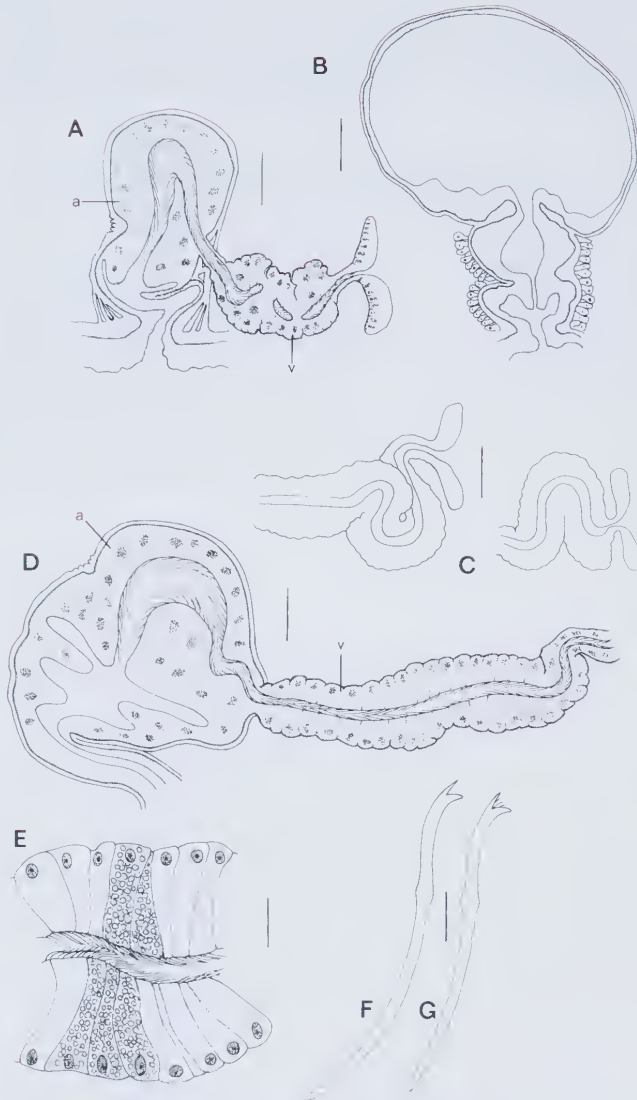


Figure 1 *Ainudrilus nharna* Pinder and Brinkhurst: A, male genitalia of holotype; B, spermatheca of holotype; C, folded vasa deferentia of WAM V4159 and V4166; D, male genitalia from WAM 37-98; E, section through vas deferens of WAM V4156, showing glandular nature of lining cells; F, ventral chaeta; G, dorsal chaeta. Scale lines: A–D 50 μ m; E–G, 20 μ m.

of Walpole, Western Australia, 34°41'02"S 116°51'13"E, 9 September 1996 (WAM 1-99 to 4-99).

Other Material

Not previously listed. All specimens from the south-west of Western Australia, collected by the authors with D.J. Cale or J.M. McRae and held by CALM. Calyerup Creek, west of Fitzgerald River National Park, 33°56'11"S 119°03'56"E, 12 September 1998; Dale River at Lupton's Bridge, 32°18'08"S 116°41'16"E, 29 October 1997; Dam on Gorge Rock,

SE of Corrigin, 32°27'29"S 117°59'53"E, 22 October 1997; Hamersley River, Fitzgerald River National Park, 33°53'25"S 119°51'39"E, 12 September 1998; Jimperding Brook at Lover's Lane, 31°35'32"S 116°21'43"E, 28 October 1997; Lake Bryde, 30 km SW of Newdegate, 33°21'14"S 118°49'26"E, 3 October 1997; Lake Coomelberrup, 10 km SE of Dumbleyung, 33°24'36"S 117°47'01"E, 05 Nov 1998; Lake Dulbining, 40 km E of Narrogin, 32°54'24"S 117°36'49"E, 24 October 1997; Melaleuca swamp 30 km NW of Hopetoun, 33°49'40"S 120°24'20"E, 11

September 1998; Melaleuca swamp in Paperbark Nature Reserve, 21 km SE of Corrigin, 32°24'58"S 118°05'51"E, 25 October 1999; Peenebup Creek, 10 km S of Ongerup, 34°06'02"S 118°32'12"E, 27 September 1998; Lake Pleasant View, Manypeaks, 34°49'51"S 118°10'59"E, 29 September 1998.

Material listed in Pinder and Brinkhurst (2000) newly deposited with WAM. Thomas Spring, south-west of Augusta, 34°21'00"S 115°09'35"E, 17 September 1996 (WAM V4159); northern tributary of Collier Creek on Cemetary Road, Walpole, 34°58'30"S 116°45'12"E, 11 September 1996 (WAM 4160); Frankland River at Roe Road Ford, 34°41'02"S 116°51'13"E, 9 September 1996 (WAM V4156-4158).

Remarks

This species was described and illustrated in Pinder and Brinkhurst (2000) but re-examination of new and previously documented material has revealed some new features and intra-specific variation for some characters. Pinder and Brinkhurst (2000) noted 4–7 penial chaetae per bundle but up to 10 per bundle have now been observed. As noted for the two new species, one or both of the spermathecal ampullae of *A. nharna* sometimes lie in IX, though still with pores anteriorly on X. The vasa deferentia of this species are ciliated, with the lining tissue consisting of a single layer of tall cells filled with vacuoles (Figure 1E) indicating glandular activity. The lumen of the vasa deferentia is generally difficult to follow and was wrongly interpreted as being folded vertically in the holotype (partly because of confusion with the ovary, which is normally closely associated with the vas deferens) but is actually only slightly folded horizontally (Figure 1A). The vasa deferentia vary from fairly straight (Figure 1D) to moderately folded (Figure 1C) in dissected specimens. The atria of the sectioned holotype appear fairly erect (Figure 1A), whereas in dissected and slide mounted specimens (e.g. Figure 1E), including specimens collected with the holotype, the atria appear more squashed. This is probably due to compression under the coverslip, although the lower part of the atrium and the ejaculatory duct appear to be eversible (seen protruding from the male pore in some specimens) so the shape of the atria will depend on the degree of contraction. Despite the real or apparent plasticity of the shape and arrangement of the atrium and vas deferens, all specimens attributed to *A. nharna* have the characteristic short spermathecal duct with the constriction close to the pore (Figure 1B), and have chaetae of the same size and form (Figure 1G, H) and so are considered to be conspecific.

A record of this species from Lake Walbyring near Narrogin (Pinder and Brinkhurst, 2000) was considered to be a northern outlier from other records listed in the same publication, but the new

records listed above show that the species is widespread in the south-west, including the central and southern wheatbelt and south-coast and occurs in a wide variety of wetlands. Pinder and Brinkhurst (2000) noted that *A. nharna* was present at Lake Walbyring when this wetland had a salinity of 2.8 parts per thousand (ppt) (Halse *et al.*, 2000) but was apparently absent at a later date when salinity was 20 ppt. However, the species was subsequently collected at Lake Coomelberrup and Hamersely River at salinities of 22 and 20 ppt respectively and is evidently tolerant of moderate salinity.

Ainudrilus angustivasa sp. nov.

Figure 2

Material examined

Holotype

Dissected specimen, Lake Logue, 12 km SSW of Eneabba in Lake Logue Nature Reserve, 29°59'20"S 115°08'50"E, Western Australia, 27 October 1999, S.A. Halse and D.J. Cale (WAM V4145).

Paratypes

Five on slides (1 dissected, 4 whole-mounted) and several matures and immatures in alcohol, collection data as for holotype (WAM V4147-4153).

Etymology

From the latin *angustus* (narrow), referring to the thin vasa deferentia.

Description

Dimensions of preserved and slide-mounted specimens: length 7.5–9 mm, width 0.45–0.5 mm. Number of segments 42–54. Prostomium rounded. Pharynx in II and III, pharyngeal gland cells abundant, mostly on pharynx and oesophagus rather than post-pharyngeal septa. Oesophagus from pharynx to IX, stomach in X–XII (type specimens with numerous parasitic ciliates attached to interior of stomach wall). Coelomocytes patchily distributed, particularly abundant in some pre-clitellar segments, ovoid (10–15 µm) and granulated. Clitellum covering posterior third of X and all of XI and XII, least developed ventrally on XI.

Hair chaetae absent, all chaetae bifid with upper teeth slightly shorter than lower, nodulus distal. Ventral and dorsal chaetae from II, 65–75 µm, 6–9 per bundle anteriorly, 3–5 per bundle posteriorly. Penial chaetae of XI 4–8 per bundle, 65–87 µm, with simple bent ectal ends (some bifid on semi-mature specimens) and indistinct distal nodulus. Penial chaetae lying in a line parallel to each other and protruding through the body wall ventral to

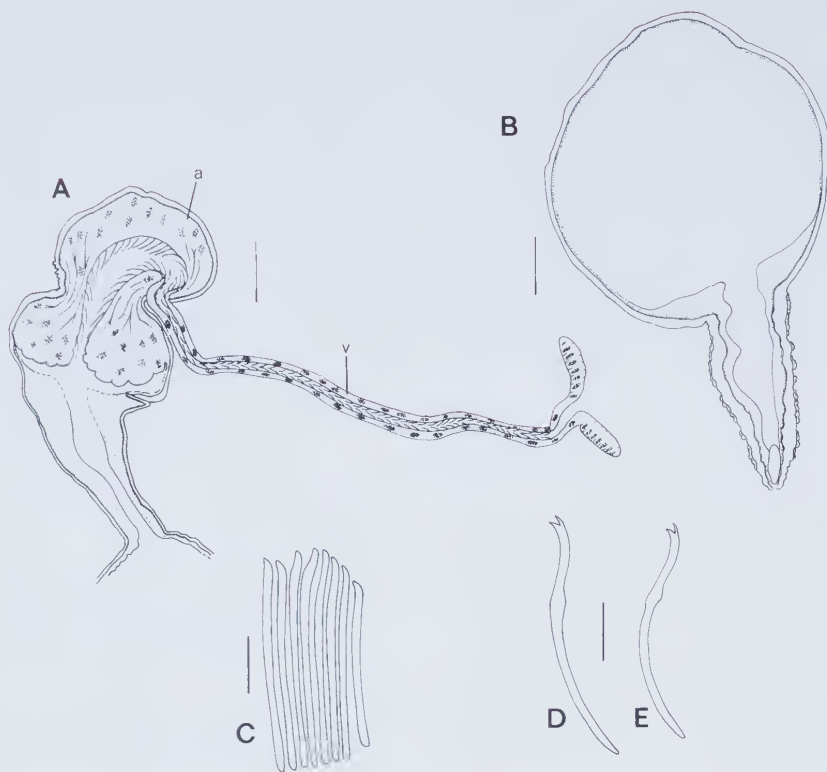


Figure 2 *Ainudrilus angustivasa* sp. nov.: A, male genitalia of holotype; B, spermatheca of holotype; C, penial chaetae; D, ventral chaeta; E, dorsal chaeta. Scale lines: A–B 50 μ m; C–E, 20 μ m.

male pores. Chaetae on spermathecal segment present but not modified.

Genitalia paired. Genital pores in line with somatic ventral chaetae, spermathecal pores anterior on X, male pores medial on XI. Male pores each a narrow slit within longitudinal depressions either side of penial chaetae. Testes and ovaries antero-ventral in X and XI respectively. Sperm sacs to VIII and XVII, egg sacs to XV. Spermathecal ampullae ovoid in IX and/or X, 210–225 μ m long, containing loose sperm, connected to pores on X via muscular ducts (130–150 \times 65–80 μ m). Ratio of length of spermathecal ampulla to duct length about 1:0.75. Ducts with lining tissue surrounded by thick circular muscle, with sparse covering of peritoneal cells. Sperm funnels on 10/11 feed narrow (14–19 μ m) non-glandular ciliated vasa deferentia which enter atria medially. Atria 115–145 μ m wide, in two parts separated by a ring of atrial muscle around the middle, upper part with thick lining tissue around broad ciliated lumen, lower part with thick lining tissue around narrower ciliated lumen, except for a more open unciliated area ectally near ejaculatory ducts. Atrial lumen not containing sperm in type material. Eversible

ejaculatory ducts narrowing between atria and pores (everted in some specimens). Prostate tissue absent. Female pores not observed.

Remarks

The lack of prostate tissue, medial entry of the vas into the atria and the bipartite atria are typical of the genus *Ainudrilus* and the numerous parallel penial chaetae are at least similar to the other freshwater forms (marine species generally have fewer, except for the type species *A. oceanicus*). The narrow vasa deferentia are unusual but also known in the marine *Ainudrilus lutulentus* (Erséus, 1984) of southern China, which was attributed to this genus by Erséus (1990) because it is 'otherwise similar to the type species' (i.e. it lacks prostate and the vas/atrial union is not apical). *Rhyacodrilus simplex* (Benham, 1903) of New Zealand also lacks prostates, which are normally present as a diffuse covering over the atria in *Rhyacodrilus*, and has thin, non-glandular vasa deferentia but the latter curl around the atrium and enter it more apically. *Ainudrilus angustivasa* differs from the remaining two species from Western Australia in the lack of hair chaetae and can be distinguished from other

Australian freshwater species, which all lack hairs, by the thin vasa deferentia and the morphology of the other chaetae, see Brinkhurst (1982, 1984) and Erséus (1997).

Lake Logue is a fresh to brackish lake fringed by Melaleuca and Acacia trees. It usually dries seasonally, although occasionally contains water for several years. At the time of sampling the water was moderately coloured at 280 TCU, pH was 7.83 to 8.18 and salinity was 1.1 ppt.

Ainudrilus ngopitchup sp. nov.

Figure 3

Material examined

Holotype

Dissected specimen, Ngopitchup Swamp, in Water Reserve 2184, 21.5 km south-west of Kojonup, 33°57'27"S 117°20'32"E, Western Australia, coll. A.M. Pinder and J.M. McRae (WAM V4154).

Paratype

Whole-mounted specimen, collection details as for holotype (WAM V4155).

Etymology

Named for the type locality.

Description

Both specimens with post-clitellar segments missing so length unknown. Width of slide mounted specimens at IX 0.34 mm (holotype) and 0.46 mm (paratype). Prostomium rounded. Pharynx in II and III, pharyngeal gland cells mostly on pharynx and oesophagus in IV–VI. Oesophagus from pharynx to IX, stomach in X–XII. Coelomocytes sparse, ovoid (about 10 µm long) and granulated. Clitellum from ½X to end of XII.

Anterior ventral chaetae 4–6 per bundle from II, 85–100 µm, bifid with upper tooth thinner and slightly shorter than upper, nodulus distal. Anterior dorsal bundles each with 4–5 long (235–330 µm) thin hairs and an equal number of crotchet chaetae of similar dimensions and form to ventral chaetae but with fine pectinations on some. Penial chaetae of XI 3–5 per bundle with simple bent ectal ends, about same length as somatic ventral chaetae, lying in parallel to each other and protruding through the body wall ventral to the male pores. Chaetae on spermathecal segment present but not modified.

Genitalia paired. Genital pores in ventral chaetal line. Spermathecal pores anterior on X, male pores medial on XI. Male pores each a narrow slit in depression lateral to penial chaetae. Testes and ovaries antero-ventral in X and XI respectively. Spermathecal ampullae ovoid, 210–260 µm long with loose sperm, connected to pores via long

muscular ducts (245–330 × 50–75 µm), ratio of ampulla to duct about 1:1.3. Duct with narrow lumen, surrounded by thick lining tissue then circular muscle and a continuous layer of peritoneal cells. Junction of duct and spermathecal ampulla particularly muscular with circular muscle forming a sphincter just ectal to duct-ampulla union. Spermathecal ducts of paratype penetrating septa 9/10 and 10/11, with one ampulla in IX and one in XI. Holotype with at least one ampulla in XI prior to dissection. Sperm funnels on 10/11 feed broad (up to 50 µm) ciliated, possibly glandular, loosely folded vasa deferentia. Exact position of atrium/vas deferens union not visible but presumably medial. Atria 85–120 µm wide, in two parts separated by a ring of muscle tissue, ental part with thick lining tissue around a broad ciliated lumen and ectal part with upper half filled with lining tissue around narrow ciliated lumen and lower half forming a broad unciliated lumen. Atria without sperm in type specimens. Ejaculatory ducts narrowing towards pores. Prostate tissue absent. Female pores not observed.

Remarks

The lack of prostate tissue, broad vasa deferentia and the bipartite atria are all typical of the genus *Ainudrilus*. The only other *Ainudrilus* to possess hair chaetae are *A. nharna* and three marine species (*Ainudrilus brendae* Erséus, 1997, *Ainudrilus piliferus* Erséus, 1997 and *Ainudrilus taitamensis* Erséus, 1990). The marine species differ from both *A. ngopitchup* and *A. nharna* in that *A. brendae* has only two small straight penial chaetae per bundle and has ventral chaetae with upper teeth much longer than the lower, and the other two have long tubular atria. The long spermathecal ducts readily distinguish the new species from *A. nharna*. The chaetae of *A. ngopitchup* are also slightly shorter than those of *A. nharna*.

The type locality, Ngopitchup Swamp, is a shallow perched seasonal sedge swamp with sandy clay sediment. At the time of sampling the water was moderately coloured at 280 TCU, pH was 8.47 and salinity was 0.58 ppt.

DISCUSSION

Apomorphies uniting species of *Ainudrilus* are the lack of prostate (presumably lost independently in *Rhyacodrilus simplex* and other genera) and the non-apical entry of the vasa deferentia into the atria. The type species, *A. oceanicus*, has vasa deferentia lining cells that are clearly glandular, as in *A. nharna*, which suggested to Baker (1982) that this species was not closely related to *A. fultoni* (then in *Rhyacodrilus*) and *Rhyacodrilus simplex*, which he observed to have non-glandular vasa deferentia. *Rhyacodrilus fultoni* was transferred to *Ainudrilus* by

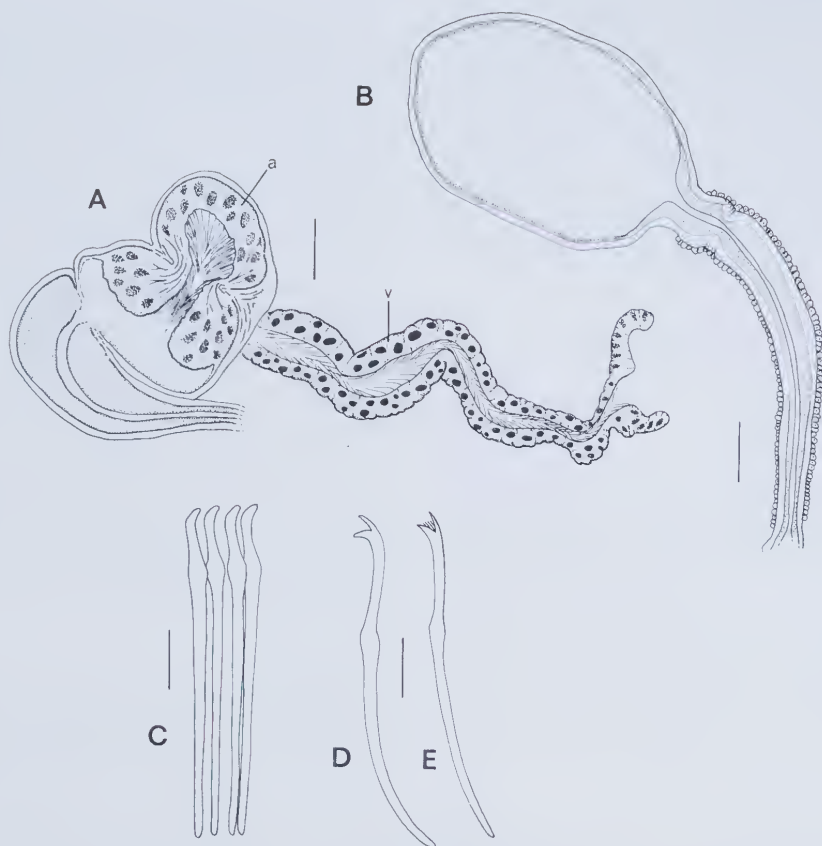


Figure 3 *Ainudrilus ngopitchup* sp. nov.: A, male genitalia of holotype; B, spermatheca of holotype; C, penial chaetae; D, ventral chaeta; E, dorsal chaeta. Scale lines: A–D 50 μ m; E–G, 20 μ m.

Erséus (1990) on the basis of its lack of prostate and non-apical atrial vas/union. Other species (*A. lutulentus* and *A. gibsoni*) with these features, but also with vasa deferentia that are not clearly glandular, have now also been included in the genus (Erséus, 1990). In fact, *A. fultoni* has vasa deferentia with an amorphous appearance, due to the thick lining tissue, and thus appears intermediate in form between *A. angustivasa* and *A. nharna*/*A. oceanicus*, whether glandular or not. Baker suggested that *A. oceanicus* has atria with thin lining tissue because the glandular role normally performed by the atrial cells was being performed by the vasa deferentia. However, *A. nharna*, which also has clearly glandular vasa deferentia (Figure 1F), has atrial lining tissue as well developed as that of *A. angustivasa* which has a thin, non-glandular vasa deferentia. This suggests that there is no correlation between the glandular development of the atria and vasa deferentia.

Both of the new species are known from single freshwater localities in the agricultural south-

west of Western Australia, where a large proportion of freshwater wetlands are threatened or already affected by secondary salinisation and hydrological disturbance. The salinity tolerances of the new species are unknown but both appear to be uncommon compared to *A. nharna*, which has been found in many wetlands and rivers throughout the south-west and is known to occur in water up to 22 ppt. Neither of the localities for the new species (Ngopitchup Swamp and Lake Logue) is threatened by salinity, as the former is perched above the surrounding landscape and the latter lies in a coastal sandplain with low salinity groundwater. However, the new species highlight the conservation value of wetlands, such as these, that are likely to maintain a diverse freshwater fauna in a region broadly affected by salinity.

ACKNOWLEDGEMENTS

The biological survey of the wheatbelt is part of

the State Salinity Strategy. Field work was undertaken with Jane McRae and David Cale and samples were sorted by Jane McRae, Melitta Penniford and Edyta Jasinska. We thank Ralph Brinkhurst and Christer Erséus for advice about the gut protozoa in *A. angustivasa*.

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Morphological variation in *Miniopterus pusillus* and *M. australis* (sensu Hill 1992) in southeastern Asia, New Guinea and Australia

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Abstract – The morphology of 366 specimens of small (forearm <45 mm; cranial mastoid width <7.9 mm) *Miniopterus* from Indonesia, Philippines, New Guinea and Australia was examined, with the assistance of univariate and multivariate statistical analyses.

Four species (*M. pusillus*, *M. australis*, *M. paululus* and *M. shortridgei*) are recognised. Each of these species differentiates into recognisable forms, mostly named, but a new subspecies is described for *M. paululus* from Selaru island. Indeterminate subspecies are recognised for *M. pusillus* from Alor, Roti and Seram islands; *M. australis* from Kai island; and *M. shortridgei* from islands in the Outer Banda Arc and Wetar island.

There was no marked sexual dimorphism among populations of these species, except in cranial height, where males were larger.

These are the first records of *M. pusillus* on Lombok, Sumbawa, Alor and Roti islands; and of *M. shortridgei* on Madura, Lombok, Sumbawa, Alor, Roti, Semau, Savu, Wetar and Selaru islands.

INTRODUCTION

According to Hill in Corbet and Hill (1992), the small species of *Miniopterus* in eastern Indonesia, Philippines, New Guinea and Australia which have a forearm length of less than 45 mm and a mastoid width less than 7.9 mm, comprise only the two species: *M. australis* Tomes, 1858 and *M. pusillus* Dobson, 1876. Hill (1983) tabulated several cranial, dentary and external body measurements of a number of populations of *M. australis* and *M. pusillus*. He stated that these species were sympatric over much of their distributional overlap. Where they occur together they can be distinguished by "the slightly greater external size of *pusillus*". However, according to Hill (1983) the literature contains many examples of these two species being misidentified.

A number of taxa have been recognised among the small species of *Miniopterus* in or adjacent to Indonesia, Philippines, New Guinea and Australia. These are listed below, along with their type localities:

Miniopterus australis australis Tomes, 1858 – Loyalty islands (but see Hill 1983: 171–173)

M. australis shortridgei Laurie and Hill, 1957 – Kalipoetjang, Tji – Tandoei R., south Java

M. a. minor Laurie and Hill, 1954 – Kalipoetjang, Tji – Tandoei R., south Java

M. tibialis (Tomes, 1858) – Ambon island, Maluku Tenggara

M. paululus Hollister, 1913 – Guimaras island, Philippines

M. macrocneme Revilliod, 1914 – New Caledonia and Loyalty islands

M. witkampii Sody, 1930 – Lobang Ipoe, Koetai, eastern Kalimantan, Borneo

M. pusillus Dobson, 1876 – Nicobar island

M. solomonensis Maeda, 1982 – Malaita and San Christobal, Solomon islands

There has been considerable confusion as to the taxonomic relationships among these taxa. For example Tate (1941) stated that "*witkampii* is a synonym of *pusillus*" and "*macrocneme* from Loyalty islands is apparently synonymous with *australis*". However, Petersen (1981b) and Hill (1983) associated *macrocneme* with *pusillus*, while Maeda (1982) associated *macrocneme* with the *Miniopterus fuscus* group of species.

Hill (1983) and Hill in Corbet and Hill (1992) considered *tibialis*, *witkampii*, *paululus*, *shortridgei* and *solomonensis* as subspecies of *M. australis*.

Tate (1941) considered *australis* synonymous with *paululus*; an opinion supported by Sanborn (1952) and considered possible by Hill (1983). Sanborn (1952) also thought it likely that *tibialis* was a synonym of *australis*. Petersen (1981a) disagreed somewhat and suggested that *paululus* and *shortridgei* were distinct from *australis*. Maeda (1982) and Koopman (1982) considered *paululus* a species; and the former



Figure 1 Map showing locality names referred to in text.

author placed *shortridgei* in synonymy with *paululus*.

Expeditions throughout Java, Nusa Tenggara and Maluku Tenggara by staff from the Western Australian Museum and Museum Zoologicum Bogoriense between 1987–1994 resulted in an extensive collection of small *Miniopterus* that were representative of *M. australis* and *M. pusillus* (*sensu* Hill in Corbet and Hill 1992). These specimens came from the islands of: Java, Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Kai, Selaru (Tanimbar), Timor, Semaui, Roti, Savu and Seram. These recent collections, in conjunction with existing collections from Borneo, Philippines, Papua New Guinea and Australia (Queensland and New South Wales), (see Figure 1 for collection localities) allow for a fresh appraisal of the taxonomy of small *Miniopterus* in this region. This paper reports on such an appraisal, particularly with the view of evaluating the uncertain taxonomic status of most populations and particularly of the previously unreported populations from Madura, Lombok, Sumbawa, Moyo, Alor, Wetar, Selaru, Semaui, Roti and Savu islands (Figure 1).

MATERIALS AND METHODS

For the morphometric analyses, 366 adult *Miniopterus* specimens from Java, Borneo, 13 islands in Nusa Tenggara and Maluku Tenggara, Philippines, Papua New Guinea and Australia were measured and analysed statistically, using both univariate and multivariate analyses.

Adult condition was judged to be when there was no swelling of the epiphyses of the wing metacarpals or phalanges. Adults were further subdivided into young adults (no wear at distal end of upper canine, or if worn dentine not exposed) and old adults (worn upper canine with dentine exposed).

The measurements (all in mm) were recorded from each specimen using vernier calipers as follows: GSL, greatest skull length; BCL, basicranial length; PL, palatal length; ICD, intercochlear distance; MW, mastoid width; MFB, mesopterygoid fossa breadth; CH, cranial height; LIB, least interorbital breadth; ZW, zygomatic width; BB, braincase breadth; C¹M³, upper maxillary tooth row cusp length; C¹C¹, distance between upper canines at basal labial surface; M³M³, distance between

upper third molar cusps, at labial surface; M^2L , upper second molar cusp length; M^2B , upper second molar cusp breadth; I_1M_3 , lower tooth row cusp length and DL , dentary length from condyle to anterior most point; SVL , snout to anus length; TVL , distal point of tail to anus length; EL , ear length; TIB , tibia length; FA , forearm length; $D2-5MC$, digits 2-5 metacarpal length; and $D3P1-3$, digit 3 phalanx 1-3 length.

Sexual dimorphism of 17 cranial, dentary and dental characters (referred to collectively as skull characters) and 12 external body characters of *Miniopterus* specimens was investigated by standard multiple regression (where all effects were assessed simultaneously) of each character on sex and population, with skull and external body characters run separately. Specimens preserved and lodged in the Western Australian Museum's collection from each island, and from Queensland and New South Wales (Australia) were regarded as separate populations. Additionally two distinct forms of small *Miniopterus* were recognised *a priori* as occurring on some islands (Java, Lombok, Sumbawa, Alor, Selaru, Semaui, Roti and Seram). Where this occurred, each form on the island was considered a separate population. These forms were clearly recognisable as a larger and smaller form.

Only the populations represented by both the two adult age types and both sexes present were included in these analyses. For the skull characters these were: Java (large form), Lombok island (small), Lombok island (large) Sumbawa island (small), Semaui (small), Savu, Selaru (small) and Queensland. For the external characters these populations were: Borneo, Sumbawa (small), Lombok (large), Semaui (small), Savu, Selaru (large), Queensland and New South Wales. The difference in the populations used in these analyses results from damage to skulls but not external body characters, or the converse. Graphical inspection of raw data using plots from regression analyses gave no indication of heteroscedasticity.

After first examining for the influence of adult age and/or sex on characters Discriminant Function Analyses (DFA) were run separately for measurements of skull and external characters. Characters that were age or sex dependent, or which had a significant interaction between age and sex, or which had a number of missing cases, were excluded from these analyses.

Populations, as identified above, that had clearly overlapping clusters in discriminant function space were combined as a group. Groups so recognised were then run again with DFA but using a subset of five most influential characters; these subsets were chosen so as to minimise the value of Wilks' Lambda (How *et al.* 1996). In all cases this subset of five characters provided a similar grouping of islands to that when the DFA used the full set of

characters. For this reason only the DFA based on such a subset of characters are presented.

Statistical analyses were performed using SPSS-PC+ (Norusis, 1986).

Specimens examined were from a number of museums. These museums are denoted by a prefix code before the specimen number as follows: WAM, Western Australian Museum; JM, Queensland; M, Australian Museum; and CM, CSIRO, Australia. Most specimens have both a skull and spirit carcass; those affixed with 'S' have a skull only and with 'E', spirit carcass only.

RESULTS

Multiple regressions

Because of the number of associations tested, the level of statistical significance is set at $P < 0.01$.

Skull characters – There were significant interactions in the full model in two characters: palatal length (sex, age, population and sex, population) and M^2 breadth (age, population). Only cranial height was sexually dimorphic with males of all populations being on average larger ($F_{1,104} = 7.304$, $P = 0.008$). Age was not significantly associated with any character. All characters differed significantly at $P < 0.001$ between populations, except greatest skull length; the characters with the highest F values were C^1M^3 length, M^3M^2 distance C^1C^1 distance and dentary length (Table 1a).

External body characters – There were no significant interactions in the full model, nor was there any significant association of any of the characters with either sex or age. However, all characters were highly significantly ($P < 0.001$) associated with population, particularly tibia length and digit 3 and 5 metacarpal lengths (Table 1b).

Discriminant Function Analyses (DFA)

(a) *Skull characters* – five skull characters were omitted from all DFA. Two of these were omitted because a number of individuals had missing values (mesopterygoid fossa breadth and zygomatic width), two because of significant interactions between main effects (palatal length and M^2 breadth) and cranial height and one because it was sexually dimorphic.

A DFA using a subset of five of the remaining 12 characters (M^3M^2 distance, braincase breadth, C^1M^3 length, C^1C^1 distance and dentary length) was run for all populations. This analysis extracted four significant functions which explained a total of 98.6% of the variation and allowed 40.4% of specimens to be allocated to their correct group. Three major groupings of these populations were apparent from the plot of Functions 1 and 2 (Figure 2a). Combinations of other Discriminant Functions

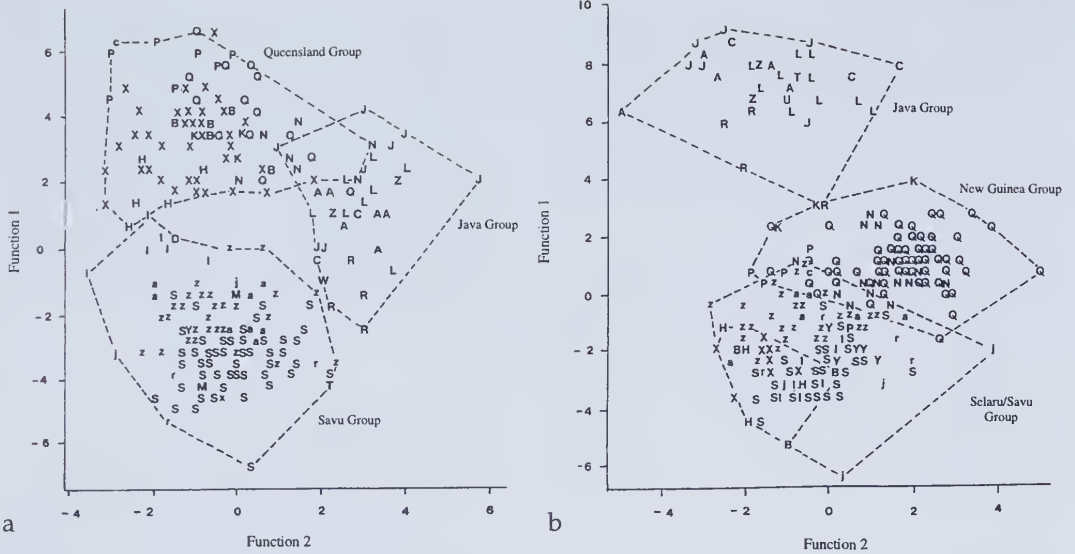


Figure 2 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and all localities for adult *Minipterus* [15 Indonesian islands, Philippines, Papua New Guinea and Australia (Queensland and New South Wales separately)]. Locality codes are as follows (when two forms are on the same island the larger form is capitalised): Borneo, B; Java, J and j; Madura, D; Lombok, L and l; Sumbawa, Z and z; Moyo, M; Alor, A and a; Wetar, W; Selaru, X and x; Kai, K; Seram, C and c; Timor, T; Semau, Y; Roti, R and r; Savu, S; Philippines, H; Papua New Guinea, P; Queensland, Q; and New South Wales, N.

do not clarify further these major groups. These groups are: *Java Group* [Java (large), Alor (large form), Seram (large), Lombok (large), Roti (large) and Sumbawa (large)]; *Queensland Group* [Queensland, New South Wales, Papua New Guinea, Borneo, Seram (small form), Philippines, Kai, Selaru (large)]; and *Savu Group* [Savu, Alor (small), Madura, Java (small), Lombok (small), Moyo, Roti (small), Timor, Wetar, Selaru (small), Semau and Sumbawa (small)].

The DFA on external body characters (see below) indicated that two clear sub-groupings of populations occurred in the Queensland Group. Consequently, after dividing the Queensland Group into two Groups (New Guinea and Selaru), a DFA was run using a subset of five skull characters (see Table 2a) and the following four *a priori* population groupings: *Java Group* (as above); *New Guinea Group* (Papua New Guinea, Queensland, New South Wales, Kai and Seram (small)); *Selaru Group* [Selaru (large), Philippines and Borneo]; and *Savu Group* (as above).

This DFA extracted three significant functions. Function 1, which separated the Savu Group from the other groups, explained 83.2% of the variance (Figure 3a). The canonical variate coefficients with the highest values on Function 1 were braincase breadth, C^1M^3 length and M^3M^3 distance (Table 2a). Function 2, which separated the Java Group from

the Selaru Group, also partially separated the Java Group, explaining 15.6% of the variance. The coefficients with the highest values on Function 2 were braincase breadth, M^3M^3 distance and M^2 length. Plots of other combinations of Functions 1 to 3 did not further clarify these four groupings.

A total of 88.5% of individuals were allocated to their correct population grouping. Only four of the 115 individuals from the Savu Group were misclassified; three to the Java Group and one to the Selaru Group. Three of the 28 Java Group individuals were misclassified; one to the Selaru Group and two to the New Guinea Group. Most misclassifications were between the New Guinea and Selaru Group: with seven of 44 individuals from the Selaru Group to the New Guinea Group and seven of the 32 individuals from the New Guinea Group to the Selaru Group and five to the Java Group.

(b) *External body characters* – Snout to vent length and tail length were omitted from all DFA because these two measurements could not be recorded with the accuracy of other body measurements.

A DFA using a subset of five of the remaining characters (tibia length, digit 5 metacarpal length, digit 3 phalanx 2 and 3 lengths and ear length) was run for all populations. This analysis extracted four significant functions and allowed 46.1% of specimens to be allocated to their correct group.

Table 1 The F-values from multiple regressions on sex, age and population and their interactions for eight populations of adult *Miniopterus* (see text) from Indonesia, Philippines, New Guinea and Australia. (a) skull characters and (b) external body characters. There were no significant interactions for external body characters. Probability levels are: *, $P<0.05$; **, $P<0.01$; and ***, $P<0.001$.

Main Effects				Interactions			
Character	sex	age	population	sex. age. population	sex. age. population	sex. population	age. population
GSL	0.340	0.047	0.659	0.076	0.036	0.118	0.0310
BCL	3.639	0.297	7.206***	1.400	0.354	0.611	0.559
PL	0.016	0.430	9.126***	7.335***	0.988	3.584**	1.627
ICD	0.709	1.003	4.647***	0.912	0.181	0.878	0.516
MW	5.844*	4.870*	28.130***	0.351	0.002	1.123	0.974
MFB	2.294	0.480*	8.626***	0.934	0.475	1.809	0.753
CH	7.304**	0.409	33.762***	0.157	2.238	1.220	0.896
LIB	1.068	0.352	12.040***	1.012	1.324	1.327	0.755
ZW	3.881	1.106	40.474***	0.423	0.032	1.215	0.897
BB	3.184	0.891	32.967***	1.800	0.012	1.432	0.993
C¹M³	3.916	1.169	64.008***	0.889	1.856	1.076	2.118
C¹C¹	2.833	0.899	40.560***	0.433	0.827	2.811*	2.433*
M³M³	0.753	0.139	61.856***	0.807	2.500	1.375	1.421
M²L	0.346	0.023	15.718***	0.996	5.135*	1.606	1.680
M²B	1.720	0.962	13.997***	1.513	2.524	1.276	4.315**
I₁M₃	0.000	0.191	4.366***	0.051	0.241	0.160	0.306
DL	2.950	0.287	40.254***	0.197	0.099	1.145	0.986
d.f	1,104	1,104	7,104	3,104	1,104	6,104	6,104

Table 1b.

Main effects			
Character	Sex	Age	Population
SVL	0.084	0.414	4.921***
TV	0.164	0.003	20.452***
EL	0.001	0.175	6.257***
TIB	4.358*	2.670	110.245***
FA	0.150	0.183	52.655***
D2MC	0.040	0.352	49.097***
D3MC	1.134	1.779	75.844***
D3P1	0.005	0.243	10.850***
D3P2	2.551	2.308	32.301***
D3P3	0.000	0.004	15.092***
D4MC	0.005	0.042	5.748***
D5MC	0.245	0.419	99.903***
d.f	1,163	1,163	7,163

characters with high coefficient values on Function 1 were tibia length and digit 5 metacarpal length (Table 2b). Function 2, which partially separated the Java Group from the other groups, explained 14.1% of the variance. The characters with high coefficient values on Function 2 were tibia length, forearm length, digit 5 metacarpal length, and digit 3 phalanx 2 length. A total of 85.4% of individuals were classified to their correct population with, as expected, most misclassifications between the Savu and Selaru Groups. In the Java Group, 91% of the 104 individuals were correctly classified; misclassifications were 3% to the Savu Group and 6% to the Selaru Group. Only one of the 34 New Guinea Group individuals was misclassified (to the Savu Group). In the Savu Group, 81% of the 138 individuals were correctly classified; misclassifications were 6% to the Java Group and 13% to the Selaru Group. In the Selaru Group, 73% of the 33 individuals were correctly classified; misclassifications were 3% to the Java Group and 24% to the Savu Group.

Morphological variation within major population groups

Considerable subclustering was apparent among populations within the major population groups

Three major groupings of these populations are apparent and these are displayed in a plot of Functions 1 and 2 (Figure 2b). These major population groupings were (using the above terminology): Java Group; New Guinea Group; and Selaru Group and Savu Group (combined). However, because individuals in the Savu group were distinguishable on skull characters from the Selaru Group, the DFA was based on a subset of five external body characters (see Table 2b) and the four *a priori* groups of Java, New Guinea, Selaru and Savu. This analysis extracted three significant functions. Function 1, which explained 82.2% of the variance, separated the New Guinea Group from the other groups and partially separated the Selaru Group from the Java Group (Figure 3b). The

Table 2 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and four *a priori* population groups (Java, New Guinea, Selaru and Savu, see text) of adult *Miniopertus*. (a) skull and (b) external body characters. Character codes described in text.

Character	Function 1	Function 2	Function 3
M ³ M ³	0.4561 (4.2094)	0.5107 (4.7141)	-1.0065 (-9.2902)
BB	0.5034 (4.0535)	-0.8807 (-7.0924)	-0.0011 (-0.0090)
C ¹ M ³	0.4950 (4.8138)	0.0246 (0.2390)	0.9945 (9.6701)
M ² L	0.0671 (1.7091)	0.4871 (12.4004)	0.2347 (5.9744)
BCL	-0.3644 (-2.4652)	-0.0583 (-0.3945)	0.1357 (0.9178)
Constant	-64.9332	9.2704	-11.4014
Variance explained (%)	83.2	15.6	1.2

Character	Function 1	Function 2	Function 3
D5MC	0.4417 (0.5051)	0.8880 (1.0155)	-0.6030 (-0.6896)
TIB	0.7515 (1.3791)	-1.2043 (-2.2101)	0.0481 (0.0882)
EL	-0.0805 (-0.1534)	0.2661 (0.5069)	0.8922 (1.6992)
D3P2	-0.0606 (-0.0564)	-0.6566 (-0.6114)	0.1673 (0.1558)
FA	-0.0698 (-0.0677)	0.9035 (0.8776)	0.4292 (0.4169)
Constant	-31.9806	-20.2784	-16.5598
Variance explained (%)	82.2	14.1	3.7

(Java, New Guinea, Selaru and Savu), both in skull and or external body characters. This variation was also examined using DFA.

The Java Group

Skull characters – a DFA based on all the Java Group populations and using a subset of five skull characters extracted two significant functions which combined explained 85% of the variance with 68.6% of individuals allocated to their correct population; no clear subgroups of these populations was detected.

External body characters – a DFA based on all Java Group populations and using a subset of five external body characters (ear length, digit 3 phalanx 1-3 and digit 5 metacarpal length) extracted two significant functions in which 74% of individuals were allocated to their correct population. The

configuration of these populations in discriminant function space was very similar to Figure 4 but with a marginal overlap between the populations nominated as the western and southeastern forms on that figure. From this DFA the following population groups were recognised: *Western subgroup* (Java, Lombok, Sumbawa); *Southeastern subgroup* (Alor and Roti); and *Seram subgroup* (Seram island)

A DFA based on these three subgroups (Western, Southeastern and Seram) and using a subset of five external body characters (see Table 3) extracted two significant functions. Function 1, which explained 74.7% of the variance, separated the Seram subgroup from both the Western and Southeastern subgroups (Figure 4). All characters, except tibia length, had high canonical variate coefficients on Function 1 (Table 3). Function 2, which explained 25.3% of the variance, separated the Southeastern subgroup from both the Western and Seram subgroups. The characters with high coefficient values on Function 2 were digit 5 metacarpal length, ear length and digit 3 phalanx 1 length. A total of 94.1% of individuals were classified to their correct population subgroup. Misclassification only occurred in the Southeastern subgroup where two of the 10 individuals in this group were allocated to the Western subgroup.

Table 3 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected external body characters and three *a priori* populations subgroups (Western, Southeastern and Seram) of adult *Miniopertus* in the Java Group (see text).

Character	Function 1	Function 2
EL	0.9077 (3.1093)	0.6362 (2.1794)
D3P3	0.7261 (1.5434)	0.0583 (0.1240)
D5MC	0.9224 (0.8365)	-1.2242 (-1.1102)
D3P1	-0.6927(-1.6310)	0.5464 (1.2867)
TIB	-0.3667 (-0.3847)	0.4827 (0.5064)
Constant	-46.8639	-6.0525
Variance explained (%)	74.7	25.3

The New Guinea Group

Skull Characters – a DFA based on all populations in the New Guinea Group and using a subset of five skull characters (see Table 4a) extracted three significant functions which explained a combined

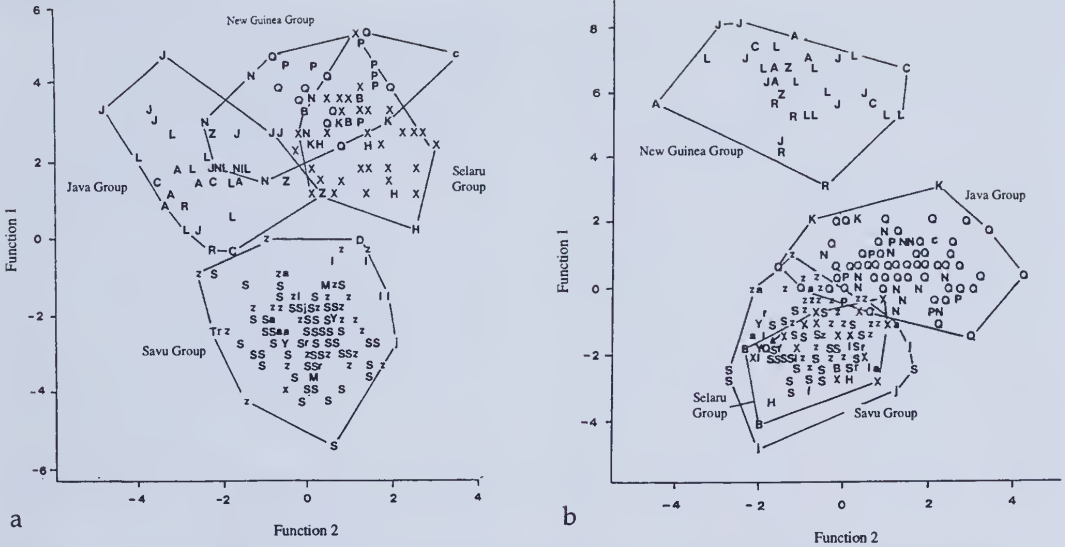


Figure 3 Plot of DFA Functions 1 and 2 based on five (a) skull (b) external body characters and four *a priori* groupings of localities (Java, New Guinea, Sclaru and Savu Groups, see text) of adult *Miniopterus*. Locality codes as for Figure 2.

97.9% of the variance. Only 77.1% of individuals were classified to their correct population subgroup. Function 1, which explained 58.5% of the variance, separated the Papua New Guinea

population from both the Kai and New South Wales populations (Figure 5a). The characters with high (>0.5) coefficient values were C¹M¹ length, dentary length and greatest skull length (Table 4a). Function 2, which explained 24.9% of the variance, separated the Kai population from the others. The character with the highest coefficient value on Function 2 was intercochlear distance (Table 4a). Function 3, which explained 14.5% of the variance, did not noticeably separate further these populations.

External characters – a DFA based on all populations in the New Guinea Group and using a subset of five external body characters (see Table 4b) extracted three significant functions which combined explained 97.7% of the variance. Only 56.7% of individuals were classified to their correct population. Function 1, which explained 65.4% of the variance, separated the Papua New Guinea population from the Kai and New South Wales populations and partially so from the Queensland population (Figure 5b). The characters with high coefficients (>0.5) on Function 1 were digit 3 phalanx 1 length, ear length and tibia length (Table 4b). Function 2, which explained 24.3% of the variance, separated the Kai population from the other populations (Figure 5b). The character with the highest coefficient on Function 2 was tibia length (Table 4b). Function 3, which explained 9.3% of the variance did not noticeably further separate these groups.

The above analyses indicated that while the Papua New Guinea population had diverged from the New South Wales population; the Queensland population was both geographically and

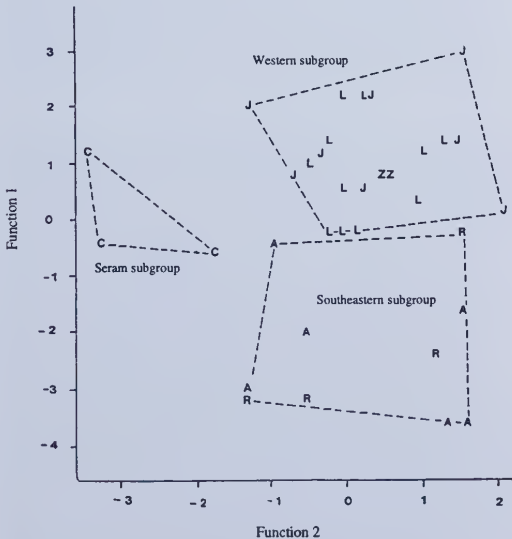


Figure 4 Plot of DFA Functions 1 and 2 based on five external body characters and all Java Group populations (see text) for adult *Miniopterus*. Locality codes as for Figure 2. Three subgroups of populations are apparent from this analysis (Western, Southeastern and Seram).

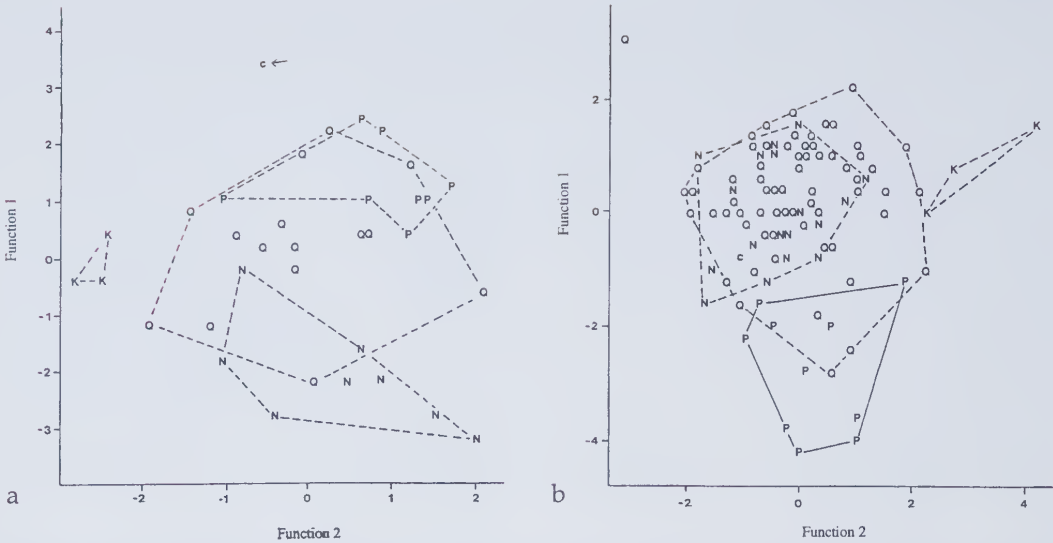


Figure 5 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and the four New Guinea Group populations (New Guinea, Queensland, New South Wales and Kai island) for adult *Miniopterus*. Locality codes as for Figure 2.

morphologically intermediate between them. The Kai population, represented by only three specimens, appeared to form a subgroup separate from the Papua New Guinea, Queensland and New South Wales populations.

The Selaru Group

Skull characters – a DFA based on the three

populations of Borneo, Philippines and Selaru as *a priori* groups and using a subset of five skull characters (see Table 5a) extracted two significant functions. Function 1, which explained 91.9% of the variance, separated all three populations (Figure 6a). All five characters had high coefficient values on Function 1 (Table 5a) which suggested that overall skull size was important in separating these

Table 4 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and four populations (Kai, New Guinea, Queensland and New South Wales) of adult *Miniopterus* in the New Guinea Group (see text). (a) skull and (b) external body characters.

Table 4a				
Character	Function 1	Function 2	Function 3	
C'M ³	0.6378 (7.4690)	0.4619 (5.4096)	-1.1766 (-13.7785)	
GSL	-0.5034 (-3.2171)	0.4439 (2.8372)	1.2120 (7.7464)	
ICD	-0.3369 (-4.7289)	0.6065 (8.5132)	-0.5549 (-7.7884)	
M ² L	0.2055 (6.5967)	-0.4442 (-14.2600)	0.3979 (12.7725)	
DL	0.6463 (4.4046)	-0.1149 (-0.7831)	0.3511 (2.3927)	
Constant	-42.0322	-53.1482	-64.9240	
Variance explained (%)	58.5	24.9	14.5	

Table 4b				
Character	Function 1	Function 2	Function 3	
D3P3	0.8337 (1.7967)	-0.0900 (-0.1940)	0.3421 (0.7371)	
TIB	0.5286 (1.3082)	0.7407 (1.8334)	-0.2608 (-0.6454)	
EL	-0.5818 (-0.9738)	-0.0746 (-0.1249)	-0.1564 (-0.2617)	
D3P2	-0.1913 (-0.2285)	-0.2253 (-0.2691)	1.0794 (1.2896)	
FA	-0.3811 (-0.4763)	0.4637 (0.5796)	0.0278 (0.0347)	
Constant	2.0761	-42.6074	-25.740	
Variance explained (%)	65.4	24.3	9.3	

Table 5 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and three populations (Borneo, Philippines and Selaru) of adult *Miniopterus* in the Selaru Group (see text). (a) skull and (b) external body characters.

Table 5a Character	Function 1	Function 2
I_1M_3	0.7940 (8.0915)	0.5475 (5.5792)
BB	-0.9966 (-7.7188)	1.0001 (7.7461)
MW	0.8575 (6.2331)	-0.4952 (-3.5995)
M^3M^3	-0.8138 (-8.5414)	0.1177 (1.2358)
C^1C^1	0.7086 (7.3221)	-0.1008 (-1.0413)
Constant	-26.8162	-67.7533
Variance explained (%)	91.9	8.1

Table 5b Character	Function 1	Function 2
EL	0.5450 (1.3966)	0.0426 (0.1091)
D3P1	-0.3955 (-0.8599)	0.8448 (1.8368)
D3P3	0.6162 (0.8501)	-0.6363 (-0.8780)
D2MC	-1.1344 (-1.2697)	-0.2616 (-0.2928)
D3P2	0.8204 (2.4340)	0.4129 (1.2249)
Constant	-28.7462	13.3848
Variance explained (%)	86.8	13.2

populations. Function 2, which explained 8.1% of the variance, separated the Borneo and Philippine populations. The characters with high (>0.5) coefficients on Function 2 were braincase breadth and I_1M_3 length. A total of 94.1% of individuals

were classified to their correct population. All individuals in the Borneo and Philippine populations and all but three of the 42 individuals from the Selaru population were correctly classified; these three Selaru individuals were misclassified to the Philippine population.

External characters— a DFA, based on the three populations of Borneo, Philippines and Selaru as *a priori* groups and using a subset of five external body characters (see Table 5b), extracted two significant functions. Function 1, which explained 86.8% of the variance, separated the Selaru population from both the Philippine and Borneo populations (Figure 6b). All five characters, except digit 3 phalanx 1 length, had high (>0.05) coefficient values (Table 5b). Function 2, which explained 13.2% of the variance, separated the Borneo and Philippine populations. The characters with high (>0.5) coefficients on Function 2 were digit 3 phalanx 1 and 3. A total of 97% of individuals were classified to their correct populations. All individuals in the Borneo and Philippine populations were correctly classified; a single Selaru individual was misclassified to the Borneo population.

The Savu Group

Skull characters — a DFA based on all populations in the Savu Group and using a subset of five characters (dentary length, M^3M^3 distance, intercochlear distance, mastoid width and C^1M^3 length) extracted four significant functions, which combined explained 98.1% of the variation. There

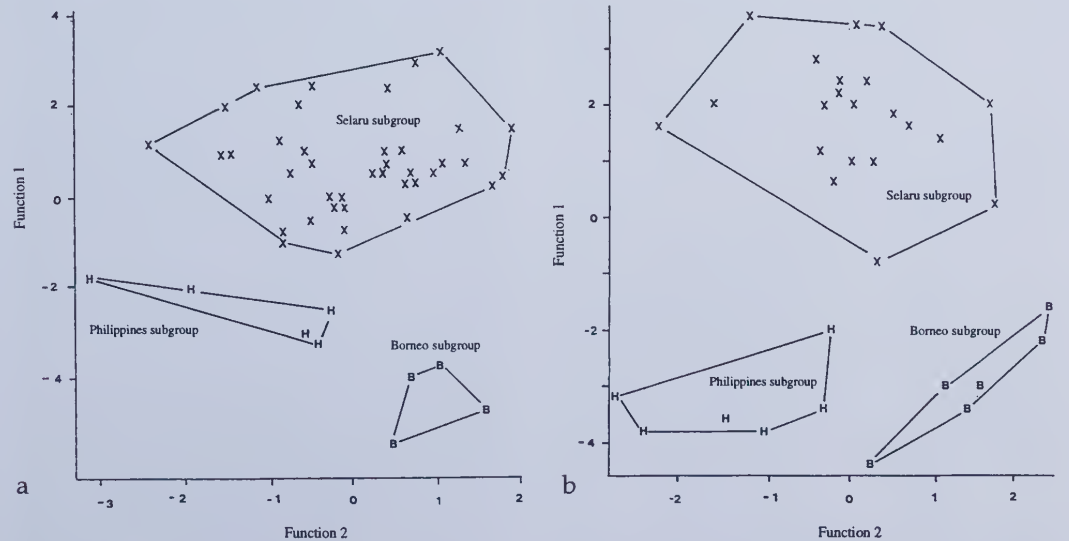


Figure 6 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and the three Selaru Group populations (Borneo, Philippines and Selaru) for adult *Miniopterus*. Locality codes as for Figure 2.

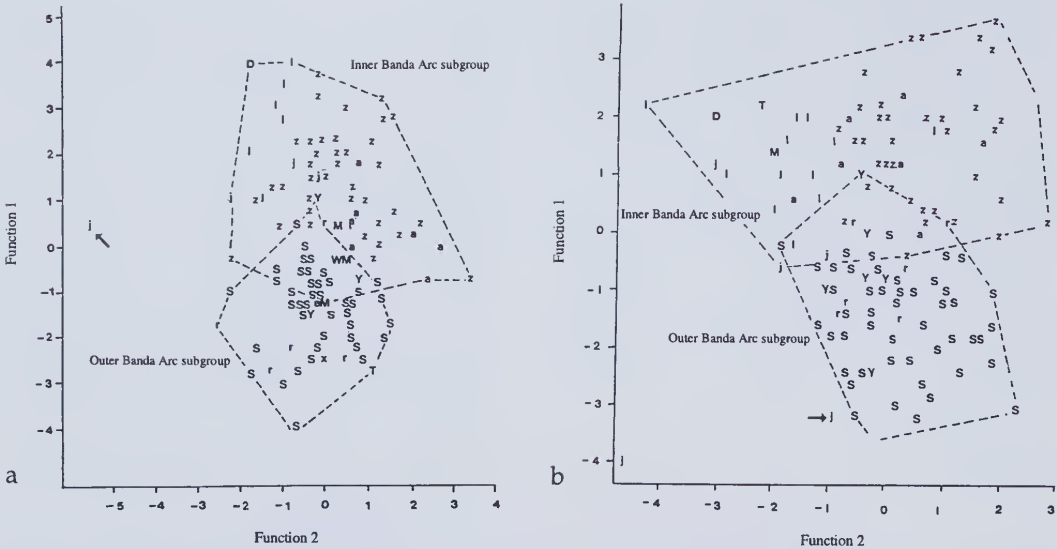


Figure 7 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and all the island populations in the Savu Group (see text) for adult *Miniapterus*. Locality codes as for Figure 2.

was, however, considerable overlap between these populations, with only 45.2% of individuals classified to their correct population. The plots of combinations of Functions 1 to 3, which combined explained 92.5% of the variance, indicated that some morphological substructuring occurs among these populations. For example, Function 1 which

explains 67.6% of the variance, separated most of the populations in the Inner Banda Arc group of islands from the populations in the Outer Banda Arc islands (Figure 7a). Plots of combinations of other functions do not noticeably clarify further these groupings.

Table 6 Standardised and unstandardised (in brackets) canonical variate coefficients from DFA based on five selected characters and two *a priori* subgroupings of the 12 island populations (Inner and Outer Banda Arc, with Wetar island included in the latter subgroup) of adult *Miniapterus* in the Savu Group (see text). (a) skull and (b) external body characters.

Table 6a	
Character	Function 1
DL	0.6507 (4.4852)
ICD	0.5579 (6.8625)
MW	-0.7147 (-5.8647)
C'M ³ L	0.6320 (8.0696)
M ³ L	0.2319 (6.1311)
Constant	-54.7709

Table 6b	
Character	Function 1
D3P2	1.0514 (1.3822)
D3P1	-0.4575 (-1.1849)
D5MC	0.9814 (1.4285)
M3MC	-0.8619 (-1.1053)
EL	-0.3023 (-0.7236)
Constant	-22.0157

A DFA based on the two subgroups identified above, namely the *Inner Banda Arc subgroup* (Java, Madura, Lombok, Sumbawa, Moyo, Alor) and the *Outer Banda Arc subgroup* (Timor, Roti, Semau, Savu, Wetar and Selaru) and using a subset of five characters (see Table 6a) extracted a significant function (Figure 8a) which classified 91.2% of individuals to their correct population subgroup. A total of 93.8% and 88.7% of individuals in the Outer Banda Arc and Inner Banda Arc subgroups, respectively, were correctly classified. Individuals that were misclassified in the Outer Banda Arc subgroup comprised the following numbers of individuals: Roti, 1; Semau, 1; and Savu, 2. Inner Banda Arc misclassifications were as follows: Java, 2; Moyo, 1; Sumbawa, 2; and Alor, 2. All characters had high coefficient values on Function 1 (Table 6a).

External characters – a DFA based on all populations in the Savu Group and using a subset of five characters (digit 3 phalanx 2, tibia length, ear length, forearm length and digit 3 metacarpal length) extracted three significant functions, which combined explained 95.6% of the variance. There was considerable overlap between these populations with only 57.6% of individuals classified to their correct populations. Plots of Functions 1 and 2 (Figure 7b) revealed most of the separation between these populations, which

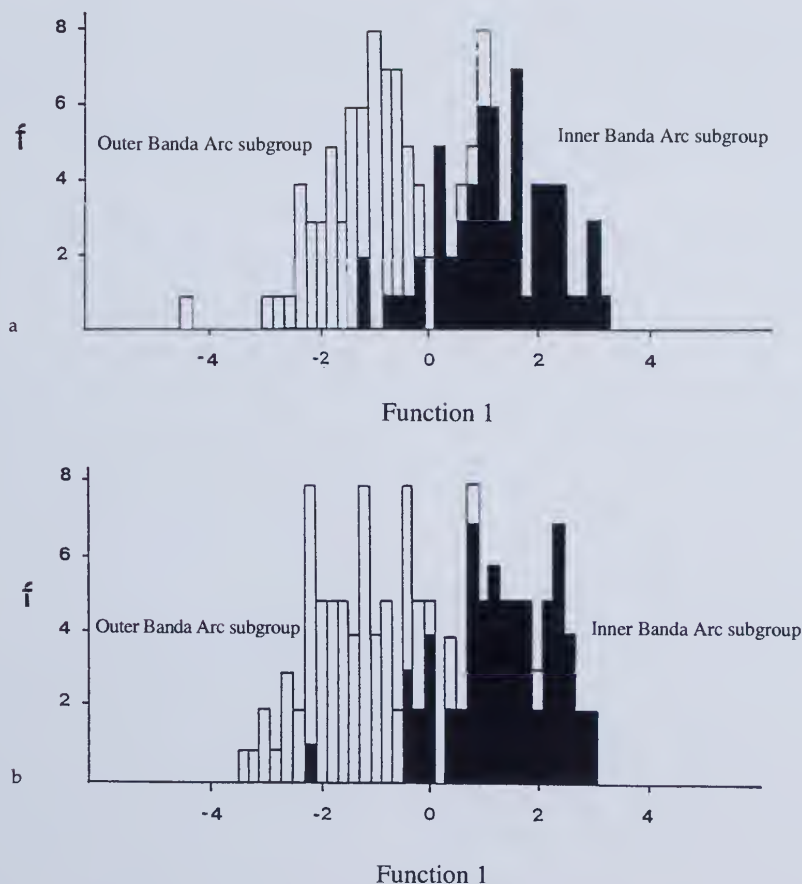


Figure 8 Plot of DFA Functions 1 and 2 based on five (a) skull and (b) external body characters and two groupings (Inner and Outer Banda Arc, with Wetar island placed in the Outer Banda Arc subgroup) (see text) for adult *Miniopterus*. Locality codes as for Figure 2.

cluster similarly to the populations that were clustered above based on skull characters.

A DFA based on the Inner and Outer Banda Arc subgroups above and using a subset of five external body characters (see Table 6b) extracted a significant function (Figure 8b) which classified 92.7% of individuals to their correct population subgroup. A total of 94.1% and 91.3% of individuals in the Outer Banda Arc and Inner Banda Arc subgroup, respectively, were classified correctly. Numbers of individuals that were misclassified in the Outer Banda Arc subgroup comprised the following: Semau, 1; Roti, 1; Savu, 1; and Timor, 1. The characters that had high coefficient values (>0.5) were digit 3 phalanx 2 length, and both digit 3 and digit 5 metacarpal lengths (Table 6b).

Summary of multivariate analysis

The combination of DFA on skull and external

body measurements of specimens of *Miniopterus* used in this study indicated the presence of considerable morphological differentiation among these island populations. Four distinct groups of populations were identified (Java, New Guinea, Selaru and Savu). The Java Group was the most distinctive and was separated from these other population groups, both in skull and external body characters, but particularly the latter. The Savu Group was separated from the remaining three populations groups on skull characters but could not be separated from the Selaru Group on external body characters. The New Guinea and Selaru Groups were separated principally on external body characters.

All four population groups are recognised as separate species. Within each of these four major population groups there was morphological differentiation, some of which is recognised as

length 19.0 (14.7–20.3) 35 v. 15.9 (14.8–17.3) 107. It also is on average smaller in all skull characters (Table 7a), except cranial height, least interorbital breadth and braincase breadth; for example, greatest skull length 13.5 (12.9–14.0) 35 v. 14.0 (13.5–14.4) 36 and C¹M³ length 5.2 (4.9–5.3) 35 v. 5.4 (5.2–5.6) 36. Also upper molar row generally shorter relative to braincase breadth (Figure 9b).

It differs from *M. paululus* in being on average larger in all external body characters except ear length; for example, forearm length 14.0 (13.5–14.4) 36 v. 37.1 (34.2–38.7) 34 and tibia length 19.0 (14.7–20.2) 35 v. 15.0 (13.9–15.6) 34. Tail to vent length absolutely larger 44.8 (39.7–51.2) 34 v. 34.8 (31.2–39.0) 34. It is on average smaller in all skull characters, except mastoid width, cranial height, least interorbital breadth and braincase breadth (Table 7a). For example, greatest skull length 13.5 (12.9–14.0) 35 v. 13.8 (13.1–14.3) 53 and cranial height 5.8 (5.6–6.3) 34 v. 5.5 (5.2–5.7) 53. Upper molar cusp row generally shorter relative to braincase breadth (Figure 9b).

It differs from *M. shortridgei* in averaging larger in all skull and external body characters. For example, forearm length 42.6 (36.5–44.3) 35 v. 36.8 (33.3–39.3) 148; tibia length 19.0 (14.7–20.2) 35 v. 15.0 (13.4–16.4) 150; greatest skull length 13.5 (12.9–14.0) 35 v. 13.3 (12.6–13.8) 135; and C¹M³ length 5.2 (4.9–5.3) 35 v. 5.0 (4.6–5.2) 137. Braincase breadth usually greater relative to upper molar cusp row length (Figure 9b).

Miniopterus pusillus pusillus Dobson, 1876

Lectotype and type locality: stated above.

Specimens examined: Indonesia; Java Island – Cibereum, 6°44'S, 107°00'E, WAM M(27160-4) 2♀ ♀ 3 ♂ ♂. Kiskenda, 7°06'S, 110°16'E, WAM M(39322, 39327, 39371) 3 ♂ ♂. Lombok Island – Bang Kang, 8°30'S, 116°10'E, WAM (M35850-54, 35857-8, 35868, 35873, 35876, 35960) 8♀ ♀, 3♂ ♂. Sumbawa Island – Batu Tering, 8°48'S, 117°22'E, WAM M31453 ♀. Desa Sangeang, 8°18'S, 118°56'E, WAM M(31547-8) 2♂ ♂.

Diagnosis

Miniopterus p. pusillus differs from *M. pusillus* subsp. A (see below) by averaging larger in all external body and skull characters, except for digit 3 phalanx length, mesopterygoid fossa breadth and M² breadth, which are subequal in length (Table 7a, b). For example, forearm length 42.8 (40.5–44.1) 21 v. 42.0 (36.5–44.3) 11; tibia length 19.2 (18.2–20.2) 21 v. 18.6 (14.7–20.0) 11; greatest skull length 13.6 (13.2–14.0) 22 v. 13.4 (12.9–13.8) 10; M³M³ distance 5.5 (5.3–5.7) 22 v. 5.3 (5.1–5.5) 10. Ear generally longer relative to digit 3 phalanx 3 length (Figure 10).

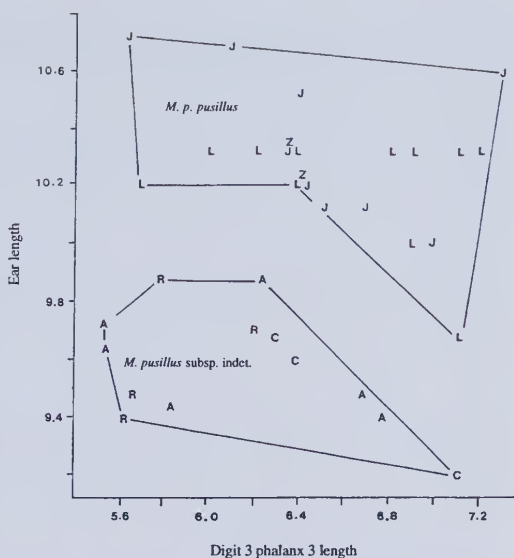


Figure 10 Plot of ear length (mm) versus digit 3 phalanx 3 length (mm) for island populations of adult *Miniopterus pusillus pusillus* and *M. p. macrocneme*. Island codes as for Figure 2.

It differs from *M. pusillus* subsp. indet. cf. *M. p.* subsp. indet. A from Seram island by averaging smaller in most external body characters, and larger in most skull characters (Table 7a, 7b). For example, forearm length 42.8 (40.5–44.1) 21 v. 43.4 (42.9–43.7) 3; ear length 10.3 (9.7–10.7) 21 v. 9.5 (9.2–9.7) 3; greatest skull length 13.63 (13.16–14.02) 22 v. 13.35 (13.27–13.42) 3 and C¹M³ length 5.20 (5.04–5.32) 22 v. 5.13 (5.08–5.15) 3. Ear longer relative to digit 3 phalanx 3 length (Figure 10).

Distribution

Lombok, Sumbawa (this study); Nicobar Islands (type locality); Madras, Thailand, Hong Kong, Java and Sumatra (Hill 1983, Hill in Corbet and Hill 1992).

Miniopterus pusillus subsp. indet. A

Specimens examined: Indonesia; Alor Island – Kalabahi, 8°14'S, 124°32'E, WAM M(37567E, 37875, 37886E, 37904-7) 7 ♂ ♂. Roti Island – Baa, 10°44'S, 123°06'E, WAM M(35357, 35359E, 35387S, 123°06'35402, 35404) 5♀ ♀. Seram island – Manusela, 3°10'S, 129°36'E, WAM M(34719, 34724, 34726) 3♀ ♀.

Diagnosis

Miniopterus pusillus subsp. indet. A and the referred specimen from Seram island differs from *M. p. pusillus* as described in the earlier diagnosis of that subspecies.

Table 7 Measurements of adult (males and females combined) *Miniopterus pusillus*, *M. australis*, *M. paululus* and their subspecies and unnamed forms and population Group and subgroup names from this study (a) cranial, dentary and dental and (b) external body characters. 0, mean; SD, standard deviation; MIN, minimum; MAX, maximum and N, sample size. Character codes defined in text.

Table 7a - Skulls		GSL	BCL	PL	ICD	MW	MFB	CH	LJB	ZW	BB	C'M ³	C'C ¹	M ³ M ³	M ² L	M ² B	I'M ³	DL
<i>Miniopterus pusillus</i> (Java Group)		\bar{x} 13.53	5.18	5.16	1.23	7.64	1.68	5.83	3.48	7.48	7.27	5.16	3.93	5.44	1.21	1.40	6.55	9.59
		SD 0.27	0.16	0.16	0.06	0.20	0.14	0.16	0.11	0.21	0.16	0.10	0.14	0.13	0.04	0.06	0.12	0.19
		MIN 12.92	4.85	4.72	1.11	7.00	1.39	5.55	3.23	6.83	6.96	4.93	3.57	5.09	1.12	1.29	6.30	9.25
		MAX 14.02	5.46	5.43	1.38	8.07	1.94	6.25	3.68	7.88	7.71	5.32	4.12	5.69	1.29	1.56	6.86	10.04
		N 35	31	33	34	35	29	34	35	30	35	35	35	35	35	35	33	35
<i>M. p. pusillus</i> (Western subgroup)		\bar{x} 13.63	5.21	5.19	1.24	7.72	1.66	5.88	3.51	7.57	7.31	5.20	3.98	5.49	1.22	1.41	6.60	9.65
		SD 0.25	0.15	0.14	0.07	0.16	0.15	0.16	0.11	0.16	0.17	0.08	0.12	0.10	0.04	0.07	0.10	0.18
		MIN 13.16	5.01	4.99	1.11	7.29	1.39	5.62	3.23	7.22	7.07	5.04	3.64	5.28	1.17	1.29	6.41	9.34
		MAX 14.02	5.46	5.43	1.38	8.07	1.94	6.25	3.68	7.88	7.71	5.32	4.12	5.69	1.29	1.56	6.86	10.04
		N 22	21	22	22	22	19	22	22	17	22	22	22	22	22	22	20	22
<i>M. pusillus</i> subsp. indet A (Southeastern subgroup)		\bar{x} 13.36	5.08	5.08	1.22	7.49	1.73	5.71	3.43	7.32	7.20	5.08	3.83	5.34	1.18	1.38	6.49	9.53
		SD 0.24	0.20	0.21	0.04	0.21	0.09	0.11	0.10	0.24	0.12	0.10	0.14	0.13	0.04	0.05	0.12	0.19
		MIN 12.92	4.85	4.72	1.17	7.00	1.58	5.55	3.32	6.83	6.96	4.93	3.57	5.09	1.12	1.29	6.30	9.25
		MAX 13.79	5.38	5.35	1.31	7.77	1.84	5.92	3.58	7.56	7.33	5.23	3.98	5.50	1.27	1.43	6.62	9.76
		N 10	7	8	9	10	7	9	10	10	10	10	10	10	10	10	10	10
<i>M. pusillus</i> subsp. indet A (Seram subgroup)		\bar{x} 13.35	5.21	5.08	1.20	7.60	1.66	5.82	3.44	7.48	7.19	5.13	3.89	5.43	1.17	1.42	6.50	9.43
		SD 0.08	0.01	0.08	0.07	0.06	0.08	0.11	0.02	0.10	0.18	0.04	0.08	0.10	0.03	0.08	0.08	0.08
		MIN 13.27	5.20	4.99	1.12	7.55	1.60	5.69	3.42	7.37	6.99	5.08	3.81	5.32	1.15	1.40	6.41	9.34
		MAX 13.42	5.22	5.14	1.26	7.66	1.75	5.90	3.46	7.54	7.34	5.15	3.96	5.49	1.20	1.45	6.55	9.48
		N 3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>M. australis</i> (New Guinea Group)		\bar{x} 14.00	5.28	5.40	1.24	7.72	1.75	5.76	3.42	7.59	7.21	5.40	3.99	5.67	1.30	1.48	6.80	10.00
		SD 0.19	0.11	0.14	0.08	0.18	0.07	0.13	0.08	0.16	0.11	0.12	0.10	0.14	0.04	0.06	0.15	0.20
		MIN 13.48	5.00	5.08	1.08	7.03	1.61	5.47	3.30	7.20	6.96	5.20	3.84	5.34	1.21	1.33	6.57	9.67
		MAX 14.44	5.46	5.74	1.39	8.02	1.87	6.02	3.60	7.91	7.41	5.63	4.27	5.98	1.38	1.56	7.12	10.38
		N 36	33	33	35	36	30	36	36	31	36	36	36	35	36	36	36	36
<i>M. a. tibialis</i> (P.N.G. subgroup)		\bar{x} 14.05	5.31	5.51	1.26	7.62	1.80	5.77	3.43	7.57	7.15	5.51	4.02	5.78	1.30	1.50	6.93	10.16
		SD 0.12	0.06	0.12	0.07	0.25	0.04	0.14	0.09	0.17	0.13	0.06	0.09	0.10	0.02	0.02	0.06	0.11
		MIN 13.94	5.24	5.36	1.16	7.03	1.75	5.47	3.32	7.30	6.96	5.44	3.90	5.65	1.27	1.47	6.85	9.99
		MAX 14.21	5.38	5.74	1.33	7.86	1.87	5.90	3.60	7.82	7.34	5.63	4.14	5.98	1.33	1.53	7.00	10.31
		N 8	7	7	7	8	6	8	8	8	8	8	8	8	8	8	8	8
<i>M. a. tibialis</i> (Queensland/NSW subgroup)		\bar{x} 14.03	5.28	5.37	1.25	7.78	1.74	5.76	3.41	7.60	7.25	5.37	3.98	5.63	1.29	1.48	6.77	9.97
		SD 0.17	0.11	0.13	0.08	0.13	0.08	0.14	0.08	0.17	0.09	0.11	0.11	0.14	0.04	0.05	0.14	0.20
		MIN 13.73	5.00	5.08	1.10	7.53	1.61	5.48	3.30	7.20	7.06	5.20	3.84	5.34	1.21	1.36	6.57	9.67
		MAX 14.44	5.46	5.57	1.39	8.02	1.87	6.02	3.57	7.91	7.41	5.56	4.27	5.91	1.38	1.56	7.09	10.38
		N 24	22	22	24	24	20	24	24	20	24	24	24	23	24	24	24	24

<i>M. australis</i> subsp. indet. (Kai subgroup)	\bar{x}	13.64	5.17	5.27	1.13	7.55	1.70	5.76	3.43	7.58	7.13	5.27	3.97	5.71	1.30	1.38	6.64	9.78
	SD	0.16	0.10	0.02	0.07	0.05	0.03	0.08	0.07	0.07	0.05	0.07	0.03	0.02	0.04	0.05	0.09	0.06
	MIN	13.48	5.06	5.25	1.08	7.51	1.68	5.69	3.37	7.53	7.08	5.21	3.94	5.70	1.26	1.34	6.57	9.71
	MAX	13.80	5.25	5.29	1.21	7.60	1.73	5.85	3.50	7.66	7.16	5.35	4.00	5.73	1.34	1.42	6.74	9.83
	N	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3	3
<i>M. a. tibialis</i> (Seram subgroup)	\bar{x}	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	SD	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
	MIN	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	MAX	14.04	5.20	5.58	1.17	7.64	1.71	5.60	3.35	-	7.03	5.63	4.05	5.87	1.38	1.49	7.12	10.23
	N	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1
<i>M. paululus</i> (Selaru Group)	\bar{x}	13.81	5.20	5.32	1.23	7.55	1.77	5.49	3.37	7.48	7.07	5.31	3.92	5.67	1.31	1.45	6.68	9.88
	SD	0.23	0.14	0.46	0.09	0.15	0.09	0.12	0.09	0.19	0.14	0.11	0.11	0.09	0.04	0.05	0.13	0.17
	MIN	13.07	4.91	4.79	1.05	7.18	1.57	5.21	3.11	6.76	6.68	5.05	3.66	5.44	1.25	1.32	6.37	9.18
	MAX	14.29	5.74	8.06	1.38	7.88	1.91	5.74	3.58	7.75	7.31	5.62	4.13	5.88	1.40	1.56	6.96	10.26
	N	53	43	43	53	53	42	53	53	50	53	53	52	53	53	53	52	51
<i>M. p. paululus</i> (Philippine subgroup)	\bar{x}	13.66	5.06	5.31	1.15	7.38	1.65	5.41	3.25	7.56	6.97	5.16	3.80	5.61	1.28	1.45	6.46	9.78
	SD	0.13	0.05	0.19	0.04	0.08	0.06	0.10	0.08	0.12	0.11	0.08	0.03	0.04	0.02	0.05	0.06	0.14
	MIN	13.49	5.00	5.15	1.11	7.28	1.57	5.30	3.11	7.44	6.84	5.05	3.76	5.56	1.26	1.40	6.37	9.58
	MAX	13.81	5.12	5.58	1.21	7.47	1.73	5.53	3.31	7.75	7.10	5.25	3.84	5.65	1.30	1.53	6.51	9.95
	N	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5	5
<i>M. p. witkampii</i> (Borneo subgroup)	\bar{x}	13.94	5.13	5.25	1.18	7.47	1.69	5.49	3.36	7.66	7.23	5.25	3.81	5.70	1.33	1.38	6.53	9.82
	SD	0.27	0.18	0.12	0.05	0.09	0.03	0.06	0.08	0.10	0.05	0.06	0.12	0.08	0.02	0.05	0.06	0.15
	MIN	13.52	4.91	5.14	1.11	7.34	1.65	5.44	3.27	7.54	7.17	5.15	3.66	5.61	1.30	1.32	6.42	9.61
	MAX	14.29	5.28	5.43	1.23	7.59	1.73	5.60	3.46	7.72	7.29	5.33	3.94	5.79	1.35	1.44	6.57	9.97
	N	5	4	5	5	5	4	5	5	3	5	5	4	5	5	5	5	5
<i>M. p. graysonae</i> (Selaru subgroup)	\bar{x}	13.81	5.23	5.33	1.24	7.58	1.80	5.50	3.38	7.46	7.06	5.33	3.95	5.67	1.31	1.46	6.72	9.90
	SD	0.23	0.13	0.52	0.09	0.15	0.07	0.13	0.08	0.20	0.13	0.10	0.10	0.10	0.04	0.05	0.10	0.17
	MIN	13.07	4.98	4.79	1.05	7.18	1.67	5.21	3.21	6.76	6.68	5.17	3.72	5.44	1.25	1.34	6.51	9.18
	MAX	14.27	5.74	8.06	1.38	7.88	1.91	5.74	3.58	7.72	7.31	5.62	4.13	5.88	1.40	1.56	6.96	10.26
	N	43	34	33	43	43	33	43	43	42	43	43	43	43	43	43	42	41
<i>M. shortridgei</i> (Savu Group)	\bar{x}	13.28	5.04	4.89	1.15	7.23	1.66	5.32	3.26	7.02	6.74	4.96	3.63	5.20	1.20	1.35	6.27	9.34
	SD	0.19	0.16	0.21	0.09	0.14	0.10	0.12	0.08	0.17	0.13	0.10	0.11	0.11	0.04	0.05	0.13	0.19
	MIN	12.57	4.37	3.47	0.92	6.60	1.40	4.96	3.08	6.28	6.32	4.61	3.38	4.86	1.10	1.16	5.79	8.81
	MAX	13.81	5.43	5.35	1.40	7.52	1.90	5.73	3.46	7.10	5.18	5.18	3.96	5.55	1.30	1.49	6.58	9.76
	N	135	119	121	134	132	124	137	137	134	137	137	135	137	137	137	135	132
<i>M. shortridgei</i> (Inner Banda Arc subgroup)	\bar{x}	13.37	5.12	4.93	1.18	7.25	1.72	5.30	3.27	7.08	6.76	5.02	3.65	5.24	1.22	1.37	6.33	9.47
	SD	0.18	0.12	0.15	0.09	0.13	0.07	0.12	0.08	0.17	0.12	0.08	0.12	0.12	0.04	0.05	0.10	0.16
	MIN	12.74	4.83	4.64	0.99	6.72	1.55	4.96	3.08	6.44	6.32	4.81	3.38	4.96	1.12	1.16	6.10	9.00
	MAX	13.81	5.40	5.35	1.40	7.52	1.90	5.63	3.46	7.53	7.08	5.18	3.96	5.55	1.30	1.47	6.58	9.76
	N	66	58	60	66	64	61	67	67	65	67	67	67	67	67	67	66	64
<i>M. shortridgei</i> (Outer Banda Arc subgroup)	\bar{x}	13.19	4.97	4.86	1.11	7.20	1.61	5.33	3.25	6.96	6.72	4.90	3.61	5.15	1.19	1.33	6.21	9.22
	SD	0.17	0.15	0.26	0.07	0.14	0.09	0.11	0.08	0.15	0.13	0.08	0.10	0.08	0.04	0.05	0.12	0.14
	MIN	12.57	4.37	3.47	0.92	6.60	1.40	5.06	3.10	6.28	6.39	4.61	3.40	4.86	1.10	1.20	5.79	8.81
	MAX	13.51	5.43	5.34	1.27	7.43	1.82	5.73	3.42	7.22	7.10	5.05	3.87	5.31	1.29	1.49	6.46	9.50
	N	69	61	61	68	68	63	70	70	69	70	70	68	70	70	70	69	68

<i>M. australis</i> subsp. indet. (Kai subgroup)	\bar{x}	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	SD	—	—	—	—	—	—	—	—	—	—	—	—
	MIN	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	MAX	38.3	38.0	10.2	15.7	39.2	34.6	36.1	10.2	27.8	6.4	34.5	31.9
	N	1	1	1	1	1	1	1	1	1	1	1	1
<i>M. paululus</i> (Selaru Group)	\bar{x}	41.6	34.8	10.5	15.0	37.1	32.4	33.5	9.2	24.6	5.4	32.2	29.8
	SD	1.9	2.2	0.6	0.4	0.8	0.8	0.8	0.5	0.9	0.6	0.8	0.8
	MIN	37.0	31.2	9.6	13.9	34.2	29.9	31.0	8.0	22.3	4.3	29.2	27.3
	MAX	45.1	39.0	11.5	15.6	38.7	34.3	35.5	9.9	26.5	6.7	34.1	31.1
	N	33	34	33	34	34	34	34	34	34	34	34	34
<i>M. p. paululus</i> (Philippine subgroup)	\bar{x}	40.8	35.3	9.7	14.8	37.0	32.4	33.2	8.6	25.3	5.1	32.1	29.6
	SD	2.1	2.0	0.2	0.4	0.7	0.8	0.7	0.2	1.0	0.4	0.8	0.7
	MIN	37.0	32.5	9.6	14.2	35.8	31.5	32.4	8.4	24.2	4.7	31.0	28.4
	MAX	43.2	37.8	10.0	15.4	37.9	33.5	34.4	8.8	26.5	5.9	33.2	30.4
	N	6	6	6	6	6	6	6	6	6	6	6	6
<i>M. p. witkampii</i> (Borneo subgroup)	\bar{x}	40.9	34.5	10.0	14.7	36.3	31.5	32.6	8.7	24.2	6.1	31.4	29.0
	SD	1.7	2.8	0.2	0.5	1.1	1.0	0.9	0.6	1.4	0.5	1.2	0.9
	MIN	38.2	31.2	9.6	13.9	34.2	29.9	31.0	8.0	22.3	5.4	29.2	27.3
	MAX	43.1	38.6	10.3	15.2	37.1	32.3	33.4	9.3	26.0	6.7	32.4	29.8
	N	6	6	6	6	6	6	6	6	6	6	6	6
<i>P. graysonae</i> subsp. nov. (Selaru subgroup)	\bar{x}	42.1	34.8	10.9	15.2	37.4	32.7	33.9	9.5	24.5	5.3	32.4	30.0
	SD	1.9	2.2	0.5	0.3	0.6	0.6	0.6	0.3	0.7	0.4	0.6	0.6
	MIN	38.4	31.9	9.9	14.4	36.5	31.4	32.9	8.9	23.5	4.3	31.5	28.7
	MAX	45.1	39.0	11.5	15.6	38.7	34.3	35.5	9.9	25.6	6.0	34.1	31.1
	N	21	22	21	22	22	22	22	22	22	22	22	22
<i>M. shortridgei</i> (Savu Group)	\bar{x}	39.9	37.2	9.7	15.0	36.8	32.6	33.4	9.1	24.5	5.6	32.1	30.0
	SD	2.16	3.5	0.4	0.5	1.0	1.1	0.9	0.4	1.1	0.5	0.9	0.9
	MIN	33.5	27.3	8.3	13.4	33.3	28.5	29.0	7.4	21.4	3.9	27.8	26.6
	MAX	46.3	64.0	10.8	16.4	39.3	37.9	35.5	10.2	27.4	6.9	34.3	32.0
	N	148	146	140	150	148	148	148	148	148	148	147	147
<i>M. shortridgei</i> (Inner Banda Arc subgroup)	\bar{x}	40.7	36.4	9.6	15.1	37.4	33.1	33.8	9.1	25.3	5.5	32.6	30.6
	SD	2.3	4.3	0.4	0.6	1.0	1.0	0.9	0.4	0.9	0.5	1.0	0.8
	MIN	34.0	27.3	8.3	13.4	33.3	28.5	29.0	7.4	21.4	3.9	27.8	26.6
	MAX	46.3	64.0	10.7	16.4	39.3	35.1	35.5	10.2	27.4	6.6	34.3	32.0
	N	73	72	70	73	72	72	72	72	72	72	71	71
<i>M. shortridgei</i> (Outer Banda Arc subgroup)	\bar{x}	38.7	38.0	9.8	14.8	36.2	32.1	33.0	9.0	23.7	5.7	31.7	29.5
	SD	4.7	2.3	0.4	0.3	0.6	1.0	0.6	0.3	0.6	0.5	0.6	0.5
	MIN	1.0	32.2	8.3	14.2	34.6	30.3	31.5	8.3	22.0	4.6	29.8	27.9
	MAX	42.8	43.9	10.8	15.6	37.7	37.9	34.2	9.5	25.8	6.9	32.9	30.7
	N	76	74	70	77	76	76	76	76	76	76	76	76

Distribution

Alor, Roti and probably Seram (this study) and Timor (Goodwin 1979), Ambon (Hill 1983) and possibly Sulawesi (Hill 1983).

Referred specimens

The three Seram specimens are morphologically slightly distinct from the Alor and Roti populations. However, because they are a small sample their subspecific status could not be assessed.

Remarks: *Miniopterus pusillus* from Ambon/Seram and Kai islands were thought by Maeda (1982) to represent the form *pusillus*, while Hill (1983) considered them *macrocneme*. Goodwin (1979) considered those from Timor island to be *M. pusillus*, whereas Hill (1983) placed them closer to *macrocneme*.

We tentatively ascribed specimens examined by us from Kai island to *M. australis tibialis*. These have measurements very similar to the *M. pusillus* reported by Hill (1983: Table 10) from that island.

Hill (1983) stated that *M. p. macrocneme* differed from *M. p. pusillus* by having longer tibia. In this study the Southeastern subgroup of *M. pusillus*, including specimens from Alor and Roti islands (close to Timor island) and the specimens from Seram (Seram subgroup) had tibia of a very similar length to those from the Western subgroup (Java, Lombok and Sumbawa) – that are *M. p. pusillus*.

Interestingly, the measurements listed by Hill (1983: Table 10) and Goodwin (1979) for *M. pusillus* specimens from Ambon/Seram islands and Timor island, respectively, fall within the range of measurements for the *M. p. pusillus* specimens in our Western subgroup, and are not clearly representative of the form *macrocneme*. Further, the difficulty in attributing specimens in the eastern Indonesian islands to *macrocneme* is further emphasised by the smaller cranial and dental measurements in our Table 7a, b for the Southeastern subgroup (Roti, Alor islands) and those presented by Revilliod (1914) – in his description of *M. macrocneme*. For example, greatest skull length 13.6 (13.2–14.0) 22 v. 14.2 (14.0–14.4) 4; mastoid width 7.7 (7.3–8.1) 22 v. 8.1 (8.0–8.2) 4; C¹M³ length 5.2 (5.0–5.3) 22 v. 5.6 (5.5–5.8). Tibia length, for the Southeastern subgroup specimens, however, averaged larger than for *M. macrocneme* (s.s.) 19.2 (18.2–20.2) 21 v. 18.3 (17.8–19.0) 50.

Specimens attributed by Hill (1983) to *macrocneme* from areas intermediate (Solomon and New Hebrides Islands, New Guinea) between New Caledonia/Loyalty islands and Alor, Roti, Timor and Seram appeared to indeed represent *macrocneme*. We have not examined specimens of *macrocneme* (s. s.) or sampled these 'intermediate' areas. However, we consider it probable that the forms in both the Seram and Southeastern subgroups will prove to be subspecifically

distinct from both *M. p. pusillus* and *M. p. macrocneme*.

Miniopterus australis Tomes, 1858

M. australis Tomes, 1858: 125

M. tibialis Tomes, 1858

?*M. solomonensis* Maeda, 1982

Lectotype: British Museum, Natural History No. BM(NH) 54.5.19.5, designated by Hill (1983: 172), who provides a detailed discussion of the history relating to the material examined by Tomes.

Type locality: Loyalty Islands.

Diagnosis

Miniopterus australis differs from *M. pusillus* as described in the above diagnosis of that species.

It differs from *M. paululus* in averaging larger in all external body characters, except ear length and digit 3 phalanx 2 length. For example, forearm length 39.2 (37.4–41.6) 107 v. 37.1 (34.2–38.7) 34 and tibia length 15.9 (14.8–17.3) 107 v. 15.0 (13.9–15.6) 34. Digit 5 metacarpal length greater relative to ear length (Figure 9a). Skull size very similar to *M. paululus* but averages slightly larger in all measurements except mesopterygoid fossa breadth and M² length. For example, greatest skull length 14.0 (13.5–18.4) 36 v. 13.8 (13.1–14.3) 53 and C¹M³ length 5.4 (5.2–5.6) 36 v. 5.3 (5.1–5.6) 53. Braincase breadth generally greater relative to upper molar row length (Figure 9b).

It differs from *Miniopterus shortridgei* in averaging larger in all external body and skull characters. For example, forearm length 39.2 (37.4–41.6) 107 v. 36.8 (33.3–39.3) 148; tibia length 15.9 (14.8–17.3) 107 v. 15.0 (13.4–16.4) 150; greatest skull length 14.0 (13.5–14.4) 36 v. 13.3 (12.6–13.8) 135; and C¹M³ length 5.4 (5.2–5.6) 36 v. 5.0 (4.6–5.2) 137.

Miniopterus australis tibialis (Tomes, 1858)

Vespertilio tibialis Tomes, 1858: 126–127

Holotype: Stated by Tomes (1858: 126) to be exhibited in the Leyden Museum, where it is supposed to still be located (Tate 1941: 575).

Type locality: Ambon ([Amboyna) island, Maluku Tenggara, Indonesia.

Specimens examined: Australia; New South Wales – Bonalbo Colliery, 28°44'S; 152°37'E, CM 877, ♂, S. Bungawalbin, 29°02'S; 153°17'E, AM M22797, ♀, E. Cangai, 29°30'S; 152°29'E, AM M(10920, 12721) 2 ♀ ♀, E. Glenreagh, 30°03'S; 152°59'E, AM M12722, ♀, E. Kempsey, 31°05'S; 152°50'E, CM 1831-2, ♀, ♂, S. Limeburners, 31°18'S; 152°57'E, AM M(21446, 21456, 21465, 21476), 3 ♀ ♀, ♂, E. Macquarie, 29°29'S;

150°07'E, AM M9026-7, ♀, ♂, E. Nimbin Rocks, 28°37'S; 153°12'E, CM (10851-3, 10857-9), 3 ♀♀, 3 ♂♂. Tooloom, 28°37'S; 152°25'E, CM (871, 873-6), 3 ♀♀, 2 ♂♂. Unknown locality, CM921, ♀, E.

Queensland – Barretts Lagoon, 18°03'S; 145°58'E, QM JM8255, ♂, E. Blue Lagoon, 22°44'29"S; 150°38'17"E, CM19095, ♂. Bracewell, 23°54'S; 150°54'E, QM JM(436, S, 437) 2 ♂♂. Bribie Island, 26°57'S; 153°07'E, QLD JM1943E, ♂. Brisbane, Camp Mt, 27°24'S; 152°54'E, QM JM (6870E, 6871) ♀, 1 Sex Unknown. Buthen Buthen, 13°23'S; 143°27'E, QM JM (2450, E, 2473, 2474E), 3 ♂♂. Cape York, Iron Range 165 kms NE of Archer River, 12°44' S; 143°15' E, AM M(16084-5, E) ♀, ♂ Cape York, Rocky River, 13°49'S; 143°28'E, CM 4487, S, ♂. Chillagoe, 17°09'S; 144°31'E, CM 10841, E, ♂. Crab Camp, 22°38'45"S; 150°43'46"E, ANWC19073, S, ♂. Creek on Atherton Rifle Range, 17°16'S; 145°29'E, AM M1680, E, ♂. Creek South of Coen, 14°06'S; 143°12'E, AM M(16082, E, 16086-91, E) 3 ♀♀, 4 ♂♂. Herberton, Extenuate Mine, 17°26'S; 145°25'E, QLD JM(8420 E, 8421, 8422 E, 8423, 8424 E, 8425, 8426 E, 8429 E) 2 ♀♀ 6 ♂♂. Kuranda, 16°49'S; 145°38'E, CM(5924, 5925-6 E, 5932 E) 3 ♀♀, ♂. Lake Barrine, 17°15'S; 145°38'E, Qld JM1450 E, ♂. Mount Boldy, 4 km West of Atherton, 17°16'S; 145°29'E, AM13610 E, ♀. Oakleigh Colliery, Glencoe section, 27°39'S; 152°36'E, Qld JM416 E, Sex Unknown. Old Irishman Mine, 19°00'S; 146°17'E, Qld JM(1675, 1676 E, 1677, 1678-1680 E), 6 ♀♀. Ravenswood, 20°06'S; 146°53'E, CM(15869 E, 15870-1), 2 ♀♀, ♂. Rockhampton, 23°23'S; 150°30'E, Qld JM(6863-6869, 6873-4 E), M(16451 E, 16794 E), 6 ♀♀, 3 ♂♂, 2 Sex Unknown. Rosella Plains, 18°25'S; 144°28'E Qld JM(2940-1 E), ♀, ♂. Thornton Peak, 16°10'S; 145°23'E, AM M(13293, 13300-5 E), 3 ♀♀, 4 ♂♂. West Claudie Range, 12°44'S; 143°17'E, Qld JM2400, E, ♂. Wombah Railway Tunnel, Via Gin Gin, 25°00'S; 151°57'E, CM(5970, 5972-3, E), 2 ♀♀, ♂. Wongabel State Forest, 17°19'S; 145°29'E, AM M16083, E, ♂. Locality Unknown, 597 E, ANWC 164525, ♀ 1 Sex Unknown.

Papua New Guinea – Putei CM (1990S, 1995E, 1997E, 1998, 1999E, 2000E, 2002, 2010S, 2020S, 2030E, 2031S, 2032E, 2040, 2043S, 2047E) 7 ♀♀, 8 ♂♂.

Seram island, Indonesia: Manusela, 30°10'S, 129°36'E, WAM M34722, ♂.

Diagnosis

Miniopterus australis tibialis differs from *M. australis* subsp. indet. from Kai island in that both Australian and New Guinea specimens have a shorter tibia 15.9 (14.8–16.9) 93 and 15.9 (15.2–16.5) 10, respectively, *v.* 17.1 (16.9–17.3) 3 and a generally shorter forearm length 39.1 (37.4–40.8) 93 and 39.7 (38.8–40.4) 10, respectively, *v.* 41.1 (40.8–41.6) 3. Most other wing measurements are also smaller (Table 7b). Most skull characters are larger (Table

7a). For example, both the Australian and New Guinea specimens have a longer greatest skull length 14.0 (13.7–14.4) 24 and 14.1 (13.9–14.2) 8, respectively, *v.* 13.6 (13.5–13.8) 3.

Distribution

Queensland, New South Wales (Australia), Papua New Guinea and Seram (this study), Ambon (type locality) and probably Sulawesi, Batchian island, Aru island, Beu island, Mayabit Bay, Waigeo, West Irian (Hill 1983).

Remarks

Tomes (1858) described *Vespertilio tibialis* from five specimens, but he noted that it differed little from *Miniopterus blepotis* except that it is a "trifle smaller, and moreover appears to ... differ remarkably in all the specimens in having the extremity of the tibia perfectly free for nearly a third of its length". He provides measurements for one of these specimens as (*in.* and *lin.* converted to mm) lengths of: head and body 63.5; head 14.8, ear 7.4; tragus 4.2; forearm 39.2–40.2; and tibia 14.8. Measurements for the other three adult male specimens from the Nicobars are provided in Dobson (1871). Sanborn (1952: 107) considered that the appearance of the extremity of the tibia in the specimen described by Tomes (1858) almost certainly resulted from the interfemoral membrane not being pinned out such that it curls up along the tibia giving the impression of a "slender shank".

Miniopterus australis subsp. indet.

Three specimens from Desa Elat, Kai island [5°39'S, 132°59'E; WAM M42885 (♀); WAM M42724 (♀) and WAM M42749 (♀)] are distinguished from *M. australis tibialis* as described in the above diagnosis. These specimens are most clearly distinguished by their long tibia (Table 7a, b). They may warrant recognition as a separate subspecies but a larger sample of specimens is required to evaluate their taxonomic status.

Miniopterus paululus Hollister, 1913

M. paululus Hollister, 1913: 311–312

M. witkampii Sody, 1930: 272–273

Holotype: United States National Museum No. 105493. Adult in alcohol, skull removed, collected in December 1887, by J.B. Steere.

Type locality: Guimaras islands, Philippines.

Diagnosis

Miniopterus paululus differs from *M. pusillus* and *M. australis* as described in the above diagnoses for these species.

Miniopterus paululus differs from *M. shortridgei* in averaging larger in all external body and skull characters except digit 3 phalanx 3 length (see Table 7a, b). For example, forearm length 37.1 (34.2–38.7) 34 v. 36.8 (33.3–39.3) 148; ear length 10.5 (9.6–11.5) 33 v. 9.7 (8.3–10.8) 140; greatest skull length 13.8 (13.1–14.3) 53 v. 13.3 (12.6–13.8) 135; and C^1M^3 length 5.3 (5.1–5.6) 53 v. 5.0 (4.6–5.2) 137. Ear length generally longer relative to digit 5 metacarpal length (Figure 9a); and upper molar cusp row generally longer relative to braincase breadth (Figure 9b).

Remarks

Revilliod (1914) diagnosed *M. australis* from *M. pusillus macrocneme* by its tragus which he stated projects anteriorly at its distal end with an almost horizontal, irregular dentate cranial margin; whereas in *macrocneme* the tragus does not project strongly forward and there is no clear dentate cranial margin. We found no such strong anterior margin in the *M. australis* available to us. Hill (1983) stated that specimens of *australis* from more western localities do not have a tragus with this dentate margin.

Miniopterus paululus paululus Hollister, 1913

Holotype and Type locality: described above.

Specimens examined: Philippine islands – Leyte island, 10°28'S, 124°45'E, WAM M29040 E, ♀. Majuyod, 9°43'S,

123°10'E, WAM M25874-5, 2 ♀♀. Negros island, 9°20'N, 123°18'E, WAM M29041-3, 3 ♀♀.

Diagnosis

Miniopterus p. paululus differs from *M. p. witkampii* in averaging slightly larger in most wing measurements (Table 7b). For example, forearm length 37.0 (35.8–37.9) 6 v. 36.3 (34.2–37.1) 6 and digit 5 metacarpal length 29.6 (28.4–30.4) 6 v. 29.0 (27.3–29.8) 6. Digit 3 phalanx 3 length generally longer relative to ear length (Figure 11a). It differs in that all skull characters, except palatal length and M^2 breadth, average smaller (Table 7a). For example, greatest skull length 13.7 (13.5–13.8) 5 v. 13.9 (13.5–14.3) 5 and braincase breadth 7.0 (6.8–7.1) 5 v. 7.2 (7.2–7.3) 5. Braincase breadth narrower relative to I_1M_3 length (Figure 11b).

Miniopterus p. paululus differs from *M. p. graysonae* subsp. nov. in averaging slightly smaller in most external body and skull characters, except tail to vent length, digit 3 phalanx 2 length and zygomatic width (Table 7a, b). For example, forearm length 37.0 (35.8–37.9) 6 v. 37.4 (36.5–38.7) 22; tibia length 14.8 (14.2–15.4) 6 v. 15.2 (14.4–15.6) 22; and greatest skull length 13.7 (13.5–13.8) 5 v. 13.8 (13.1–14.3) 43. Ear generally longer relative to digit 3 phalanx 3 length (Figure 11a).

Distribution

Majuyod and Negros island (this study), Guimaras island (type locality), Philippines.

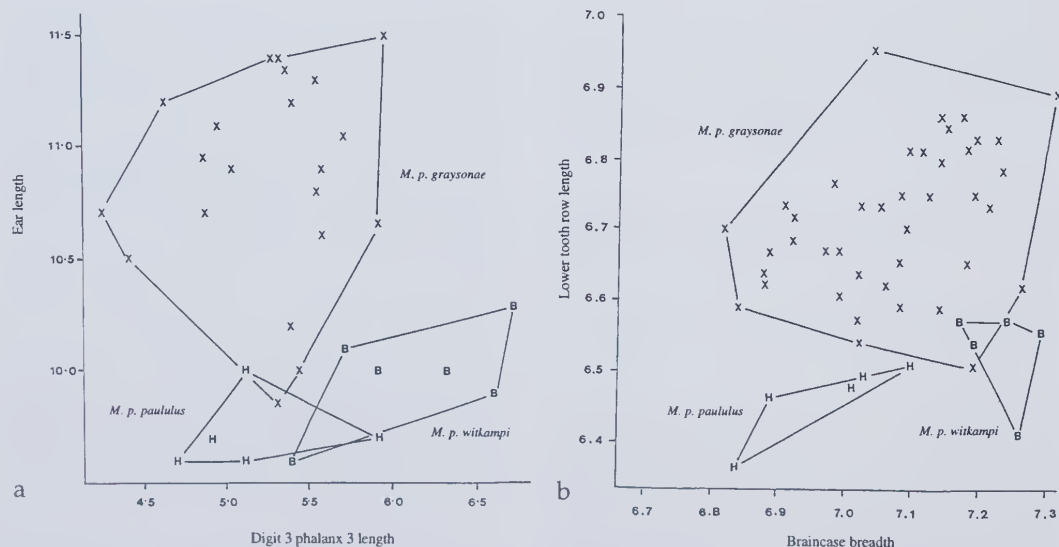


Figure 11 Plot of (a) ear length (mm) versus digit 3 phalanx 3 length (mm) and (b) lower tooth row length (mm) versus braincase breadth for island populations of adult *Miniopterus paululus paululus*, *M. p. witkampii* and *M. p. graysonae* subsp. nov. Island codes as for Figure 2.

Remarks

The forearm length of the type specimen of *M. p. paululus* fall within the range of our measurements of this taxon, but the measurements of the digit 3–5 metacarpal length and most of the skull measurements of the type, except I_M3 , are smaller than those presented herein (see Hollister 1913).

Miniopterus paululus witkampii Sody, 1930

M. witkampii Sody, 1930: 272–273

Holotype: The Sody Collection. Ex. Muzeum Zoologicum Bogoriensis No. 422, adult male, collected 24 January 1928.

Type locality: Lobang Ipoe, Koetai, East Kalimantan, Borneo island.

Specimens examined: Borneo Island – Gomantong, Sabah, 5°31' N, 118°04'E, WAM M (26002-6, 26007 E) 3 ♀♀, 3 ♂♂.

Diagnosis

Miniopterus p. witkampii differs from *M. p. paululus* as described in the above diagnosis.

It differs from *M. paululus graysonae* in averaging smaller in all external body characters, except digit 3 phalanx 3 length (Table 7b). For example, forearm length 36.3 (34.2–37.1) 6 v. 37.4 (36.5–38.7) 22 and tibia length 14.7 (13.9–15.2) 6 v. 15.2 (14.4–15.6) 22. Ear length shorter relative to digit 3 phalanx 3 length (Figure 11a). It averages slightly larger in measurement of overall skull size, such as greatest skull length, zygomatic width, braincase breadth and M^3M^3 distance and slightly smaller in other skull measurements such as mastoid width cranial skull height and C^1M^3 length (Table 7a). I_M3 length generally shorter relative to braincase breadth (Figure 11b).

Distribution

Koetai, East Kalimantan (type locality), and Gomantong, East Sabah, Borneo island.

Miniopterus paululus graysonae subsp. nov.,
Kitchener

Holotype: Western Australian Museum No. M44339, adult male, weight 5.8 gm, collected by Ir Ibnu Maryanto (Museum Zoologicum Bogoriense) and Mr Ronald Johnstone (Western Australian Museum) on 28 April 1993.

Type locality: Bangruti Cave, near Adaut, Selaru island, Tanimbar Islands Group, Maluku Tenggara, Indonesia, (ca. 8°09'S, 131°08'E), at sea level.

Paratypes: Selaru Island – Adaut, 8°09'S, 131°08'E, WAM M(44319-20, 44322-4, 44325E, 44326, 44327S, 44328-9, 44330S, 44331-3, 44335E, 44336, 44338, 44340-44 S, 44346-7S, 44348E, 44350, 44351S, 44353S,

44354, 44355-7S, 44358, 44359-61S, 44362, 44363S, 44366, 44367S, 44369E, 44371, 44372-4S, 44377S) 20 ♀♀, 24 ♂♂.

Diagnosis

Miniopterus paululus graysonae differs from *M. p. paululus* and *M. p. witkampii* as described in the above diagnoses of these subspecies.

Distribution

Known only from Selaru island, Tanimbar Island Group.

Etymology

Named after Ms Jacky Grayson, who contributed greatly to this paper by removing skulls and recording external body measurements.

Miniopterus shortridgei Laurie & Hill, 1957

Miniopterus australis shortridgei Laurie and Hill, 1957: 128 (renamed)

M. australis minor Laurie and Hill 1954: 72–73

Holotype: British Museum of Natural History No. BM 9.1.5.426 (Collector's no. 1451); adult male; skin (in alcohol) and skull separate; collected by G.C. Shortridge on 3 March 1908.

Type locality: Kalipoetjang, Tji – Tandoei River, south Java.

Specimens examined: Java island – Kiskenda, 7°06'S, 110°16'E, WAM M(39334E, 39353E) ♀, ♂. Sukabumi, 7°15'S, 106°50'E, WAM M(30007, 300010-1), ♀ 2 ♂♂ Madura island – Sampang, 7°13'S, 113°15'E, WAM M39411, ♀♂. Lombok island – Bang Kang, 8°30'S, 116°10'E, WAM M(35855, 35860-1, 35863-4, 35865E, 35866-8, 35870, 35959E, 35961) 8 ♀♀, 2 ♂♂. Sumbawa island – Batu Dulang, 8°35'S, 117°18'E, WAM M (31769-72, 31773S, 31774, 31776-81, 31782S, 31783-4, 31787-5, 31796E, 31797, 31798E, 31800-8, 31812, 31813E, 31814-6, 31818, 31853E, 31854-5) 14 ♀♀, 31 ♂♂ Desa Sangeang, 8°18'S, 118°56'E, WAM M31556 ♂. Moyo island – Sebotok, 8°09' 30" S, 117°37'15" E, WAM M31906, ♀. Tangung Pasir, 8°23'15" S, 117°31'30" E, WAM M31960, ♀. Alor island – Kalabahi, 8°14'S, 124°32'E, WAM M(37518-21, 37543, 37564, 37565E, 37566, 37625, 37627) 4 ♀♀, 6 ♂♂. Roti island – Baa, 10°44' s, 123°06'E, WAM M(35358, 35388) ♀, ♂ Oeseli, 10°51'S, 123°05'E, WAM M(35498, 35500-2) 3 ♀♀, ♂. Savu island – Menia, 10°29'S, 121°55'E, WAM M(35114, 35126, 35128, 35139, 35140S, 35141-2, 35143S, 35144-6, 35147E, 35148-51, 35152S, 35153, 35154-5, 35165-6, 35168-70, 35171E, 35172, 35173E, 35175-6, 35178-9, 35218-20, 35221E, 35223-6, 35228-30, 35231E, 35232-3, 35234E, 35235-9, 35240E, 35241-3, 35245E, 35246-54, 35255E, 38 ♀♀, 30 ♂♂. Timor island – Lifuleo Oisina, 9°18'S, 123°30'E, WAM M38065, ♀. Semau island – Desa Uiasa, 10°10'S,

the former three species, their intraspecific morphology diverged sufficiently to warrant subspecific status. In the remaining species, *M. shortridgei*, two reasonably distinct forms are recognised. One of these forms is restricted to Java and the volcanic islands of the Inner Banda Arc, which are a volcanic extension of Western Sumatra and Java (Michaux 1991); the other occurs on the gondwanic islands of the Outer Banda Arc, and apparently also on Wetar island. The single specimen from Wetar island is a damaged skull only. A DFA run with a reduced set of variables, so as to include this Wetar island specimen in the analysis as an unallocated specimen, placed it with specimens from the Outer Banda Arc group of islands.

Intraspecific morphological variation in both *M. pusillus* and *M. shortridgei* appeared to be most marked in the general region of Alor and Wetar islands. Interestingly, Alor and Wetar islands, like Roma and Kambing islands, now inactive volcanically, are characterised by reef-limestone terraces uplifted to 500–800 m above sea level (see Hamilton 1979). Perhaps the more recent volcanic activity on Inner Banda Arc islands to the west of Alor island not only impacted on the habitat and faunal assemblages on those islands, but may in some way have favoured the development of a particular bat ecomorph.

The western *M. p. pusillus* (Java-Sumbawa) is larger in all characters than the eastern form, *M. pusillus* subsp. indet. A (Alor and Roti). Further, the Inner Banda Arc form of *M. shortridgei* (Java-Alor) is larger for most characters than the form on the Outer Banda Arc and Wetar island. The region of this differentiation reflects a pattern documented by Kitchener and Suyanto (1996), Kitchener, Konishi and Suyanto (1996) and Kitchener, Packer and Maryanto (1996) who examined intraspecific morphological variation in ten species of bat and a mouse in the region of southern Indonesia between Java and the Kai islands. They noted that morphological differentiation tended to occur in the eastern parts of the distributional range of the species examined, or in the Outer Banda Arc on the islands of Sumba, Roti, Savu, Semaui and Timor. The exceptions to this were two species that morphologically diverged in the western part of this region. These were *Scotophilus collinus* Sody, 1936, which had two forms that diverged between Bali and Lombok islands, and *Hipposideros diadema* (Geoffroy, 1813), which had two subspecies that interfaced between Lombok and Sumbawa islands.

The trend for *M. pusillus* and *M. shortridgei* to become smaller in overall size on the eastern and southern islands in the Lesser Sundas is also observed in seven of the ten bat species referred to above. The exceptions were *Cynopterus nusatenggara* Kitchener and Maharadatunkamsi, 1991 and

Hipposideros sumbae Oei, 1960, which increase in size, and *Scotophilus collinus* Sody, 1936 which shows no clear such trends in morphology. Kitchener and Suyanto (1996) stated that this trend for overall skull and body dimensions to change with longitude, at least for the most eastern islands of Tanimbar and Kai, which have a less severe climate, may in part be influenced by Bergmann's effect. However, within the Lesser Sundas a complex interplay of factors is likely to be involved. This is indicated by the study by Kitchener and Maharadatunkamsi (1996) on *Cynopterus nusatenggara* which showed that most cranial, dentary and external body measurements became larger to the east or on the more isolated islands, and smaller on the islands to the south. However, the cranium and teeth also were smaller on the larger (irregularly shaped) islands.

The two forms of *M. shortridgei* overlap somewhat morphologically, but not particularly so in the region where the islands in the gondwanic outer Banda Arc and volcanic inner Banda Arc are closest. This is between Alor and Timor (the placement of Wetar island in these island Arcs is not clear). For example, a few specimens from the more western islands of Java, Moyo and Sumbawa were misclassified to the Outer Banda Arc form. For this reason, these two forms are not recognised as subspecies. It may well be that examination of further specimens from the region of the interface between these forms (Alor, Timor and Wetar islands) may provide a stronger case for the recognition of them as subspecies.

While the systematic groupings of forms in this paper into species differs somewhat from that of Hill (1983), we place the forms we studied into similar subspecies taxa. We are also doubtful that the eastern Indonesian form of *Miniopterus pusillus* on Timor and associated islands and on Seram (and Ambon) represent the form *macrocneme*. However, we recognised that other taxonomic tools need to be applied to further resolve the taxonomy of this group. Our experience with this genus leads us to agree with Goodwin (1979) that resolution of the taxonomy of many forms of *Miniopterus* is exceedingly difficult because morphological differences between even sympatric species are sometimes minor and that pelage colour is of little taxonomic value.

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A new species of *Austrarchaea* (Araneae: Archaeidae) from Western Australia

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Abstract – A new species of *Austrarchaea*, *A. robinsi*, is described from the Stirling Range National Park. It most closely resembles the only other named Western Australian archaeid, *A. mainae* Platnick, in the morphology of the female genitalia, but differs in the lack of abdominal tubercles.

INTRODUCTION

Spiders of the family Archaeidae hold a special place in the minds of many arachnologists (see Forster and Platnick, 1984) – firstly, as the original species were described from fossilised remains in Baltic Amber prior to the discovery of Recent species in Madagascar, and secondly, as indicators of the ancient links between the southern continents, where the Recent fauna is known only from Australia, Madagascar and South Africa. The Australian fauna consists of four named species attributed to the genus *Austrarchaea* Forster and Platnick: *A. nodosa* (Forster), the type species, from south-eastern Queensland, *A. daviesae* Forster and Platnick from north-eastern Queensland, *A. hickmani* (Butler) from Victoria and New South Wales, and *A. mainae* Platnick from south-western Australia (Butler, 1929; Forster, 1956; Forster and Platnick, 1984; Platnick, 1991). Main (1995) recorded several juvenile archaeids from two forested localities near Pemberton in south-western Australia, but the identity of these populations will require the collection and study of adult specimens.

The collection of numerous spiders from the Stirling Range National Park by Sarah Barrett of the Department of Conservation and Land Management in 1996 yielded an adult archaeid which proved to be distinct from all of the previously named species of *Austrarchaea*. This species is named here.

SYSTEMATICS

Family Archaeidae

Genus *Austrarchaea* Forster and Platnick

Austrarchaea robinsi sp. nov.

Figures 1–4

Material Examined

Holotype

♀, Ellen Peak, Stirling Range National Park, Western Australia, Australia, 34°21'20"S, 118°19'45"E, 28 May 1996, pitfall traps, S. Barrett (Western Australian Museum T42580).

Diagnosis

Austrarchaea robinsi differs from *A. mainae*, *A. nodosa* and *A. daviesae* by the lack of abdominal tubercles (Figure 1), and from *A. hickmani* by the presence of seta-bearing tubercles on the lateral and posterior margins of the carapaceal neck (Figure 1), and the presence of a petiolar sclerite which does not fully encircle the petiole. *Austrarchaea robinsi* appears to be the sister species to *A. mainae* as both possess numerous elongate spermathecae which fan out on either side of the gonopore (Figure 3).

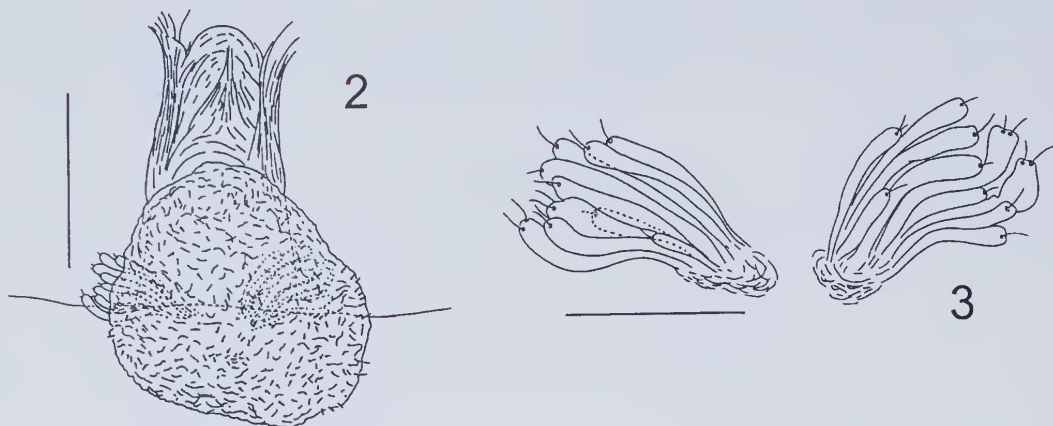
Description

Female (holotype)

Colour: carapace, chelicerae and sternum



Figure 1 *Austrarchaea robinsi* sp. nov., holotype ♀, lateral view.



Figures 2-3 *Austrarchaea robinsi* sp. nov., holotype ♀, genitalia, dorsal view: 2, entire genitalic region showing anterior and posterior receptacula, and spermathecae; 3, detail of spermathecae. Scale lines = 0.1 mm.

chestnut-brown, streaked with black markings; legs brown, with dark bands on distal end of femora, patellae, tibiae, and metatarsi; abdomen grey-yellow with sclerites all chestnut-brown. Carapace (Figure 1) with numerous white setae, generally anteriorly directed; without dorsal horns; with several rows of seta-bearing tubercles situated mostly on neck, a larger patch of tubercles situated on posterior portion of neck. Eight eyes in 2 rows; AME black, other eyes white; AMEs closer together than PMEs; ALE and PLE nearly contiguous. Chelicerae extremely elongate; without proximal lobe; distal end reflexed posteriorly; three rows of peg teeth, 17 in main row, 3 in anterior row and 1 situated posteriorly, large ridged area (presumptive stridulatory file) on subdistal region of external margin. Sternum with concave anterior margin and rounded posterior margin, lateral margins extending between coxae but not fused or adjoined to carapace. Pedipalp with small tarsal claw. Legs long and slender; formula 1423; femur II, III and, to a lesser extent, IV, with a sub-medial dorsal protuberance; tibiae I-III with 2 trichobothria, 1 sub-distal, 1 sub-basal; tibiae IV with 3 trichobothria, 2 sub-basal, 1 sub-distal; metatarsus with 1 sub-distal trichobothrium; all trichobothria associated with darkly pigmented bands on segments; each tarsus with 3 small claws. Abdomen (Figure 1) spherical, without tubercles, cuticle thin with little trace of thickening; sparsely covered with setae which are either black or white; epigastric region with four separate plates, a sub-triangular plate covering genital region, situated between two pulmonary plates, and petiolar sclerite which is only present on ventral portion of abdomen, not encircling petiole; sclerotized ridged plate (presumptive stridulatory file) above petiole; c. 16 small circular sclerites present between epigastric region and spinnerets,

with 4 pairs of larger sclerites laterally. Internal genitalia (Figures 2, 3) with c. 10 pairs of receptacula arranged in two groups, each receptaculum with thin translucent duct, terminal bulb and 1-2 distal tubules. Six spinnerets; anterior-lateral spinnerets largest, two-segmented; posterior-medial spinnerets very small; posterior-lateral spinnerets short; cololus absent.

Dimensions (mm): total length (excluding chelicerae) 4.30. Carapace length (measured at base) 1.20, width 1.10, height 1.90. Eye group width 0.87. Sternum length 0.70, width 0.44. Chelicera length 1.96. Pedipalp: femur 0.30, patella 0.17, tibia 0.35, tarsus 0.44, total 1.26. Leg I: femur 1.98, patella 0.83, tibia 1.62, metatarsus 0.89, tarsus 0.58, total 5.90. Leg II: femur 1.40, patella 0.41, tibia 1.32, metatarsus 0.58, tarsus 0.41, total 4.12. Leg III: femur 1.19, patella 0.41, tibia 1.10, metatarsus 0.49, tarsus 0.40, total 3.59. Leg IV: femur 1.81, patella 0.43, tibia 1.37, metatarsus 0.68, tarsus 0.39, total 4.68. Abdomen length 2.04, width 1.79, height (without spinnerets) 2.42.

Remarks

Austrarchaea robinsi shares with *A. hickmani* a lack of abdominal tubercles, but possesses small seta-bearing tubercles on the carapace which are absent in *A. hickmani*. As noted above, *A. robinsi* appears to represent the sister species of *A. mainae* as both possess numerous elongate spermathecae which fan out on either side of the gonopore (Figure 3, and Platnick, 1991, figure 7), a feature which is not found in any other archaetid, and which is markedly different from the eastern Australian species of *Austrarchaea*. This may indicate a separate radiation of the genus in Western Australia, based upon a shared ancestor. However, until the identity of the juveniles from the Pemberton region is ascertained, such hypotheses are speculative.

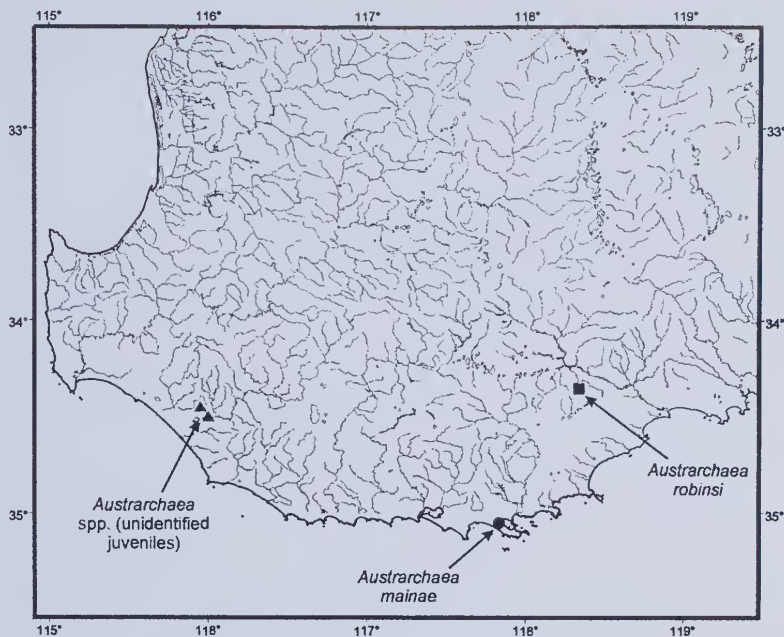


Figure 4 Map showing known distribution of *Austrarchaea* species in Western Australia: ● *A. mainae*, ■ *A. robinsi*, ▲ unidentified juveniles.

The species is currently known from only a single specimen collected in a pitfall trap placed on Ellen Peak in the eastern portion of the Stirling Range (Figure 4). The Stirling Ranges are internationally renowned for their endemic biota, which includes several endemic spiders such as the trapdoor spiders *Neohomogona stirlingi* Main (Main, 1985) and an undescribed species of *Moggridgea* (B.Y. Main, personal communication). It is highly likely that *Austrarchaea robinsi* is also endemic to the Stirling Range where it survives amongst montane heath vegetation on one or more peaks.

Etymology

This species is named for Western Australian paralympian Noel Robins, the first recipient in the Western Australian Museum's Live Forever program.

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A new Middle Devonian dipnoan from Morocco: structure and histology of the dental plates

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Abstract – A new genus and species of dipnorhynchid dipnoan, *Dipnotuberculus gnathodus* gen. et sp. nov., has been found in the Givetian of Ma'der Basin of South Morocco (Presaharian Anti-Atlas). Three palates and two mandibles are available at present, all of them incomplete. No dermal roofing bones are available to us, though the dermal skeleton of the mandible is available. Large tuberosities on the palate and the mandible, the marginal addition of small blisters around the dental plates, the growth of tuberosities away from the plate margins, the elongate surangular, the large anterior pit with openings down into the Meckelian space, the great median length of the mandible, and the modification of dental surface by thick dentine and massive bone underlying it, demonstrate that the specimens have affinities with the Emsian genus *Dipnorhynchus*. *Dipnorhynchus* is one of the most primitive genera known, but some features of *Dipnotuberculus* indicate that many changes have taken place between the Emsian and the Givetian within the Dipnorhynchidae. Relationships with other Devonian genera are outlined.

INTRODUCTION

The material on which this description is based has a collection history. In 1990, a dipnoan palate from Morocco was purchased by the Parc de Miguasha in Quebec, Canada, from a German dealer. The dipnoan was given to Richard Cloutier to study. Another limestone block contained an arthrodire is now housed in the National Museum in Paris (MHNM 02-178), and now identified as *Madiera falipouli* Lelièvre (1995). From this the conodonts indicative of early to middle Givetian age were found. In 1994, Dr Roberta Paton of the National Scottish Museum, in Edinburgh, showed Smithson a dipnoan mandible that had been obtained from a rock shop in Lyme Regis, Dorset, U.K. Recognising its similarity to the Australian *Dipnorhynchus*, Smithson sent photographs to Campbell and Barwick in Canberra. Because of the difficulties encountered by some workers who worked on bought material, it was agreed that other palaeontologists who worked in North Africa should be contacted to enquire if they had similar material. Hence Dr Paton contacted Dr Lelièvre of the Laboratoire de Paléontologie in Paris; he was aware of the specimen from Miguasha, and had prepared the other specimen with *Madiera falipouli* Lelièvre.

Subsequently, Chatterton and a postgraduate student who were working on Devonian trilobites from Morocco, bought a second palate, and obtained an incomplete mandible from an English

dealer in fossils. The dealer had been alerted by Chatterton to the possibility of finding large dipnoans in association with the possible food items such as large invertebrates, mainly because he had found *Dipnorhynchus* in association with the brachiopods *Spinella* and *Protochonetes* and several nautiloids in New South Wales. Such species had been found in association with the holotype and other specimens of *D. sussmilchi*, as well as specimens of *D. kurikae*. Both the palate and the mandible were from Djbel Issoumour near the summit of escarpment within or just below the large *Phacops* (*Drotops*) *megalomanius* phacopid bed, near Alnif, Moroccan Sahara (see Figure 1). Both of these lungfish specimens were sent to Campbell and Barwick for study, Chatterton already being familiar with the Emsian dipnoans from New South Wales. These two specimens are now in the University of Alberta Paleontological Collections UALVP 44559, 44560. Thus there are three incomplete palates, an incomplete mandible and a much more complete mandible, making up the complete collection. Lelièvre (pers. comm.) has indicated that some specimens also come from Djbel Merakib, also in the Ma'der Basin.

In the present paper we are describing the mandible in the National Museum of Scotland in Edinburgh, and the two other specimens in the University of Alberta Collection. We believe that Cloutier and Lelièvre will describe the Miguasha specimen and the new palate which is in Lelièvre's

Collection at the Muséum National d'Histoire Naturelle in Paris, plus any comments they have on the other material.

MATERIALS AND METHODS

The specimens were preserved in limestone and were etched with acetic acid. The bones were

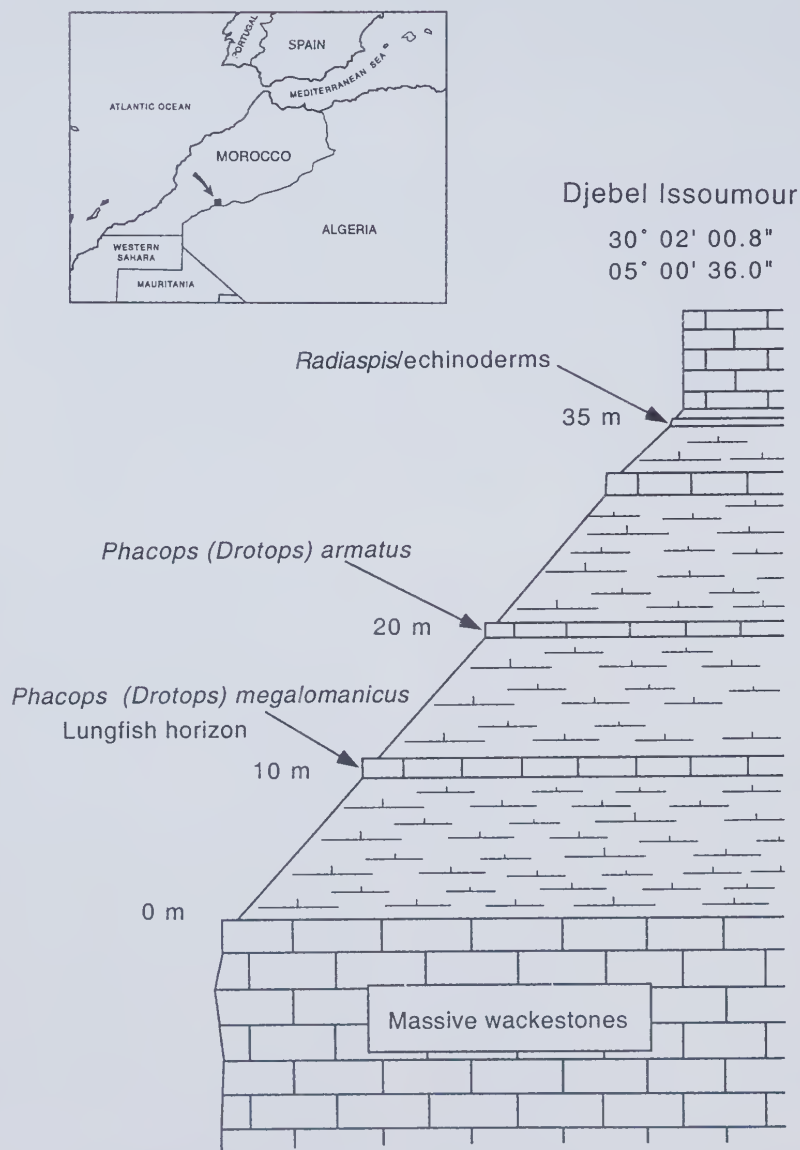


Figure 1 a. Map showing Morocco and the approximate position of the fossil locality indicated with an arrow. b. Diagram of a section through part of the Bou-Dib Formation measured by Kevin Brett in 1998. The three horizons containing trilobites are quarried for sale. Consequently, large amounts of rock are removed from these horizons, and are examined with care by local professional fossil collectors. Some of the specimens of the lungfish described here were reported to have come from the horizon containing *Phacops (Drotops) megalomanicus* Struve, on Djbel Issoumour, and were collected from somewhere close to this location. Latitude and longitude obtained from a hand held GPS unit, reportedly accurate to ca. 100 metres.

stabilised with MOWITAL, a solution which penetrates the bone and binds it together. Photographs were made by covering the surface with ammonium chloride before making the negatives.

Thin sections were cut using a thin saw blade, and mounting the surface on a glass slide. The cut surface was polished on a diamond wheel to remove the coarse scratches, and then mounted for SEM examination. The SEM work was done on a Cambridge machine, and photographs were made from the negatives. EDAX analysis was done on the SEM while the specimen was mounted for making negatives.

STRATIGRAPHY

The only published information on the ages of the specimens was Lelièvre's comment that the specimen of *Madiera falipouli* contains conodonts of early and middle Givetian age. A copy of the section at Djbel Issoumour prepared by Chatterton and his student, Kevin Brett, is included as Figure 1.

The phacopid bed is in the Bou Dib Formation (of Hollard 1974), and contains the conodonts *Polygnathus varca*, *Polygnathus foliata* and *Polygnathus linguiformis linguiformis*, indicative of an early to middle Givetian age. Middle Devonian conodonts from the nearby Ma'der region have been described by Bultynck (1985) and by Bensaid *et al.* (1985).

The Alberta mandible contained a large amount of matrix which has been processed for conodonts by Dr Robert Nicholl, and identified by Chatterton. The following species have been recorded: *Belodella devonica* (Stauffer), *Belodella resima* (Phillip), *Belodella triangularis* (Stauffer), *Icriodus brevis* Stauffer, *Icriodus obliquimarginatus* Bischoff and Ziegler, *Neopanderodus aequabilis* Telford, *Polygnathus varcus* Stauffer, *Polygnathus linguiformis linguiformis* Hinde, *Polygnathus xylus ensensis* Ziegler and Clapper. These taxa indicate that the mandible came from the lower *varcus* Subzone, of early to middle Givetian age. This is consistent with the age given by Lelièvre for the *Madiera falipouli* placoderm. Thus three of the lungfish are from rocks of the same age. The present authors do not have conodonts from the specimen in the National Museum of Scotland, but its matrix is of the same kind as has been observed on the other specimens. We have no evidence of the age of the specimen in the Miguasha Museum.

SYSTEMATICS

Suborder Dipnorhynchina Campbell & Barwick
1990

Family Dipnorhynchidae Berg 1940

Genus *Dipnotuberculus* gen. nov.

Type species

Dipnotuberculus gnathodus sp. nov. from the Middle Devonian (Givetian) of the Ma'der Basin, Morocco.

Diagnosis

Large specimens even for the Dipnorhynchina; width unusually large for an animal with this palatal length; palate formed of a single plate and shows no sign of a median suture on either its ventral or the dorsal surfaces; margin of palate with a raised rim along its posterolateral edge; anteriorly the edge carries two pairs of large isolated tuberosities on each side; a median tuberosity shows evidence of the fusion of the anterior unit on each side. Large flattened tuberosity on each side medial to the posterior marginal ridge, and two or more smaller tuberosities between these and the anterior tuberosity. Midline of palate with a single row of three or four flattened tuberosities, the largest one posteriorly and the more anterior ones much lower and shorter. Dorsal surface of the palate covered with a thin periosteal layer over coarse vesicular bone. No periosteal bone stands vertically to form an outer layer for the braincase, as it does in *Dipnorhynchus*.

Four infradentary bones present, but their edges are only clear where they intersect the posterior edge of the mandible; surangular long, extending almost to the dentary anteriorly; a shallow groove on the external surface against the infradentaries, separates off the dentary; anterior furrow well developed, but not restricted laterally; foramina in the floor of the anterior furrow leading down into the abundant symphyseal tubules. Adductor fossa large with its anterior edge formed by a contact between the surangular and the prearticular. Prearticulars join medially without a suture; three well-rounded, elongated, lateral tuberosities on the prearticular, inner surface consists of a raised rounded ridge, subdivided irregularly by narrow transverse grooves into three or four tuberosities; deep depressions with a coarse surface on the inner face of the lateral tubercles occluded with the tuberosities of the palate.

Tuberosities and the dental surface formed of a thick layer of dark-coloured dentine joined ventrally to open-textured light coloured bone; large resorption openings in the base of the dentine into which new dentine grew during ontogeny.

Remarks

Because they have been independently collected by several dealers, it is possible that all the specimens to hand are not contemporaneous, and

may not be members of the one species. Despite this, studies of the conodonts from two specimens and the knowledge that two others were from within or below the phacopid bed, demonstrate that they were also of approximately the same age. In addition, the specimens have so much in common that it is possible to write a diagnosis including all the features listed above. The genus is so distinctive that it should be easily recognised in any other areas where it appears.

The above diagnosis is extensive because it contains new data on a group not previously known from the Northern African Devonian, and comparison is made with the other members of the dipnoans from Australia. All the distinctive features are listed so that comparison with other genera will be obvious.

Etymology

dipno = referring to the group Dipnoi.

tuberculus = refers to the tuberculate dentition.

Dipnotuberculus gnathodus sp. nov.

Holotype

UALVP 44559 (mandible) University of Alberta.

Location and Horizon

Djebel Issoumour, Moroccan Sahara. From the Phacopid Bed, early to middle Givetian. The material available for the present study consists of a palate, an incomplete mandible and the dental plates of a second mandible.

Paratypes

UALVP 44560 and NSM 1993.57.1.

Diagnosis

As for genus.

Etymology

gnathodus = refers to the jaw.

Description

Palate

The palate has a broad anterior angle of about 75° (Figures 3a,b). The adult structure consists of a single entity which has no median suture. Anteriorly the lateral margins converge to a point without any excavation for the attachment of the dermopalatines. This is quite unlike *Dipnorhynchus* in which a gap occurs in the anterior edge of the pterygoids, into which the dermopalatines fit. Of course, the dermopalatines are attached to the pterygoids in that genus. In *Dipnotuberculus* there is no evidence that the dermopalatines have been

incorporated into the main bony structure. We can only conclude that they had become loose and had taken up a free position as they did in *Chirodipterus*, *Holodipterus* and other Middle and Late Devonian dipnoans. We note also that in a recent paper by Krupina and Reisz (1999), a growth series of the Late Devonian *Andrejevichthys* shows that a pair of small plates grew anteriorly to the pterygoids. In *Chirodipterus* and most other Late Devonian genera, the dermopalatines do not attach to the pterygoids but are not so far forward as those of *Andrejevichthys*; note that a small median plate, which is also free of the pterygoids, is not so far forward as in *Andrejevichthys*. In these genera we have an intermediate position between *Dipnorhynchus* and *Andrejevichthys*. Although our only example of *Dipnotuberculus* has neither a dermopalatine nor a median plate, we conclude that they would have features similar to those of *Chirodipterus*.

At the anterior end of the pterygoids is a large rounded bony mass forming a median tuberosity (Figure 3a). It shows slight evidence of having been a divided entity originally, but wear has destroyed most of the junction between the two elements. Support for the view that it was a double structure is given by the mandible in which there is a median tuberosity with a wear pit on each side (Figure 5a). Posterior to this, the margins of the palate carry two large rounded tuberosities bounded by strong furrows which pass medially beyond them. The posterior furrow is missing on the right side of the specimen. The posterior lateral edge of the palate is formed of a rounded ridge (Figure 3a). The posterior margins are incompletely preserved.

Medial to the posterior lateral ridge on the palate is a shallow groove separating off a broad flattened bony platform-like tubercle. The internal edge of the platform is steeply inclined and is bounded internally by a shallow furrow, which passes around the posterior edge of the platform becoming weaker laterally. Anteriorly the platform is bordered by a shallow furrow within which is a narrow, shallow, and sharp-edged groove. Anterior to the platform are two or three slight tuberosities making a row and joining with the median anterior tuberosity. On each side of the specimen the first and second of these tuberosities are separated by thin grooves which run between the lateral tuberosities on the plate margin. As will be shown later these furrows and grooves mark the sites where new material is added to the buccal surface.

The posteromedial part of the palate is occupied by yet another flattish tuberosity, which is not as high as the tubercles lateral to it. It is bounded laterally and posteriorly by shallow furrows, but anteriorly its edge is indefinite. Anterior to this is a low rounded ridge running almost to the anterior tuberosity. This may have carried up to three

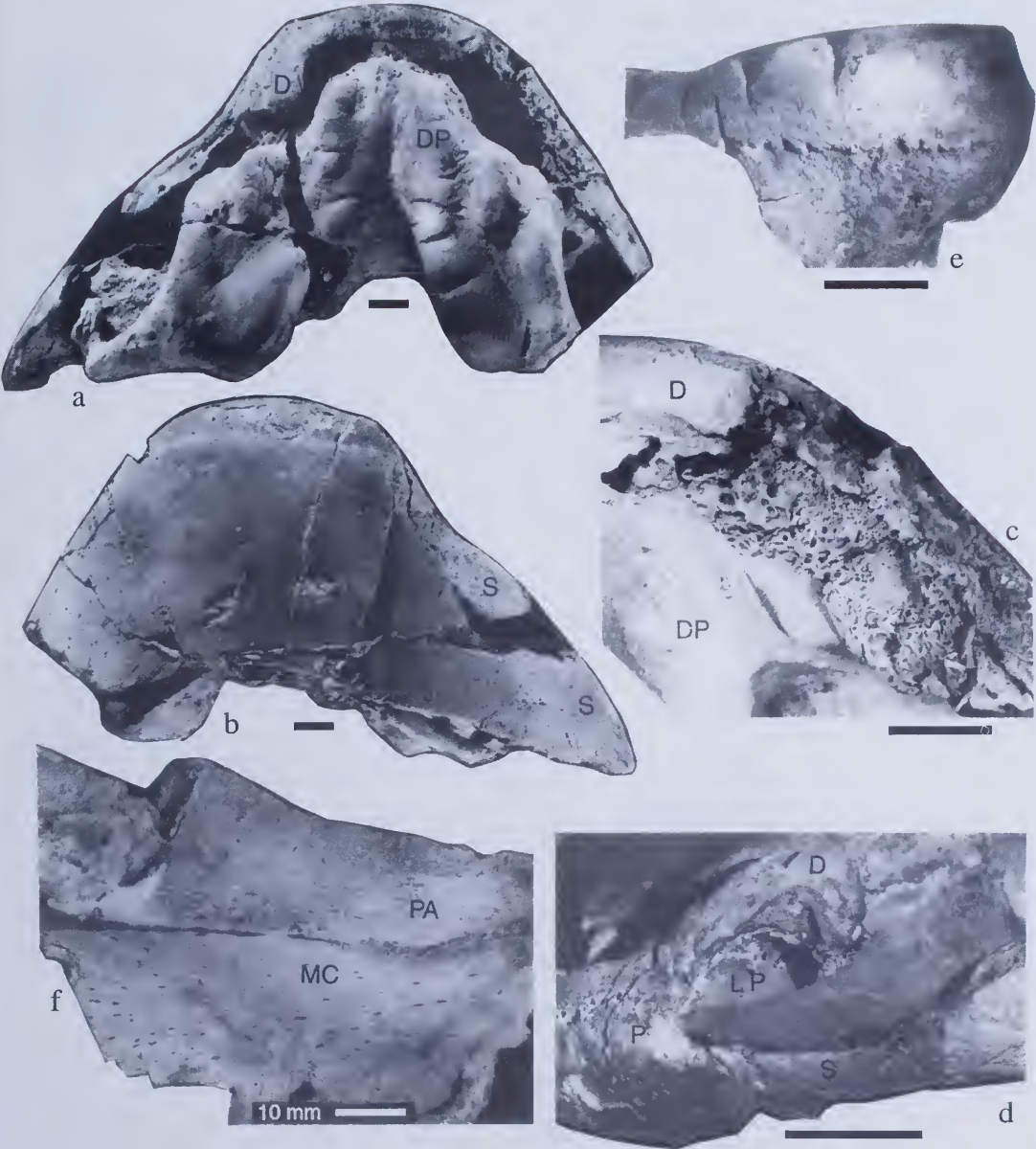


Figure 2 *Dipnotuberculus gnathodus* gen. et sp. nov. All illustrations are of the specimen NSM 1993.57.1. (a–b). Dorsal and ventral view of the specimen which was subsequently broken (D dentary; DP dental plate; S surangular). (c). View of the anterolateral corner of the broken specimen showing the complex tubules between the external dermal bones. (d). Anterolateral view of left corner showing the large pores (P) in the dentary (D), the labial pit still containing sediment (LP), and the cosmine of the surangular (S). (e). Lingual view of right dental plate showing the irregular edge of the dentine on the bone of the prearticular. (f). Internal view of the adductor space with the broken prearticular (PA) lying on the ossified Meckel's Cartilage (MC).

tuberosities, but they are very poorly defined. The furrow bounding this median group of tuberosities, continues forward as a shallowing structure almost to the posterior end of the median anterior tuberosity.

The posterior end of the palate is not preserved on our specimen, but on the right side (Figure 3c) the flattish dorsal surface approaches close enough to the buccal surface to show that there was only a thin surface of bone between them. Also on the right side

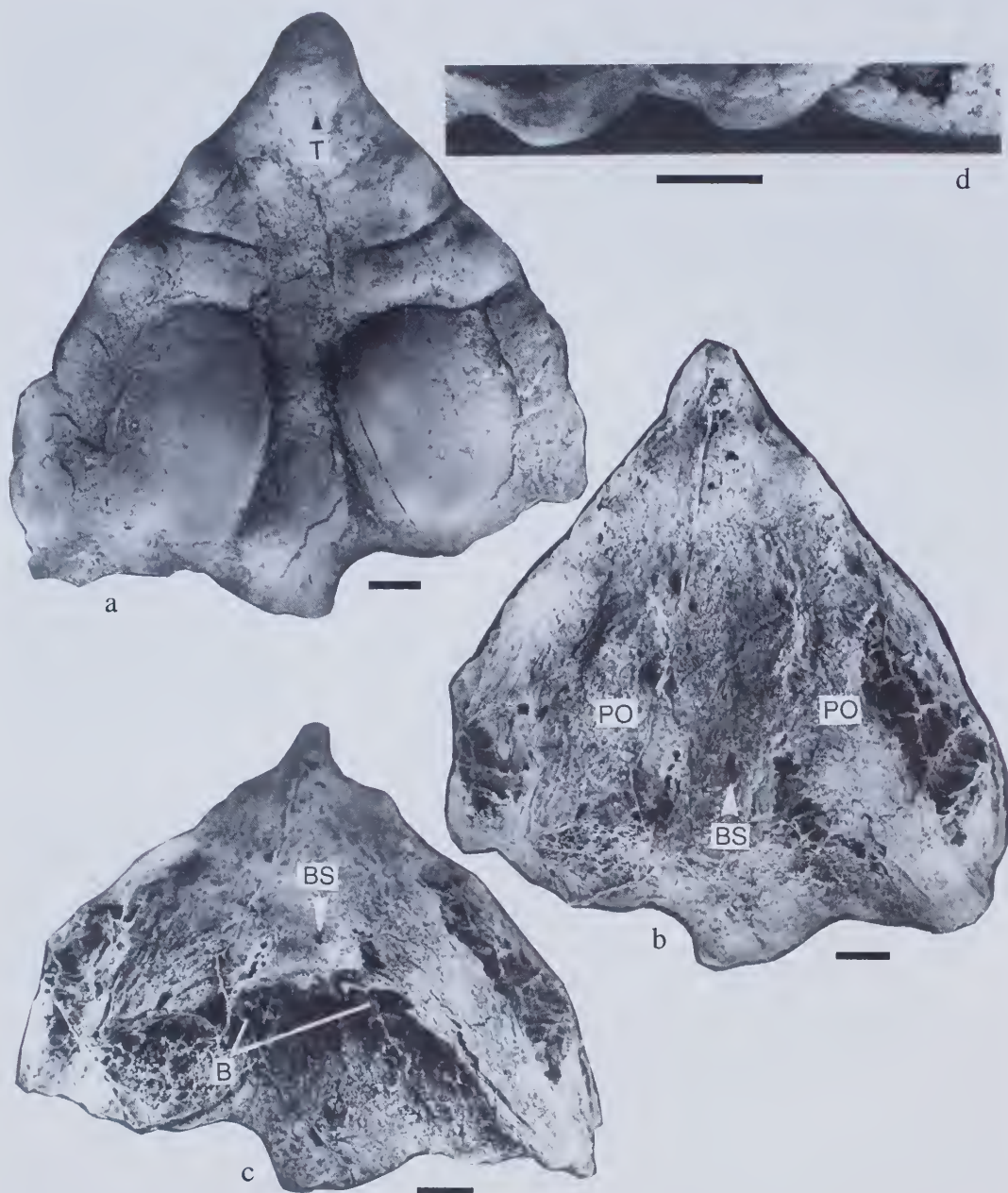


Figure 3 The palate UALVP 44560. (a–b). Ventral and dorsal views of the palate. T is the median tuberosity. In (b) note the coarse bone texture where the periosteal layer has been removed, the striated surface of the periosteal layer (PO), and the raised medial surface with the foramen for the buccohypophyseal stalk (BS). (c). Posterodorsal view of same showing the raised medial region separated from the buccal surface by coarse vascular bone (B). (d). Lateral view of the left side of the palate showing the blisters along the edge.

the lateral ridge on the buccal surface is reduced as it approaches its posterior end and turns medially. From both these features we conclude that the posterior face of the skull had no vertical ossified

ridge as found in *Dipnorhynchus*. Presumably in *Dipnotuberculus* the posterior face supporting the otic region, and separating the adductor chamber from the gill chamber, was made of cartilage.

The lateral margins of the palate are somewhat worn. The hard material along the edges is thin, and lies on a thick layer of bone which does not reach the outer edge of the hard surface. In places where the outer edge of the hard surface is preserved, especially along the surface of the tubercles, including the anterior tubercle, the pattern of deposition of the tissue is preserved. As shown on Figure 3d the additions of new tissue are flat blisters of dental tissue attached to the bony substrate. Along the more posterior ridge, the blisters are smaller. The surface of these structures show the same features as the surface of the tuberosities.

The visceral (dorsal) surface of the palate is poorly preserved, and its surface is deeply eroded posteriorly (Figure 3b,c). This exposes the very open meshwork of tissue forming the dorsal surface of the pterygoid bone, which overlies the denser vesicular layers close to the buccal surface. The dorsal surface of the pterygoid is covered with a thin layer of periosteal bone which makes a roughened dorsal surface (Figure 3b,c). Medially there is no bony connection between the braincase and this layer except posteriorly. This implies that the braincase did not sit directly on the dorsal surface of the palate, but presumably it was oriented above it by a layer of cartilage. This is in contrast with *Dipnorhynchus* in which the periosteal layer continues up the side of the braincase leaving a strong coarse bony layer along the palate after weathering (Thomson and Campbell, 1971, figure 73; Campbell and Barwick, 1985, figure 5b,c).

Anteriorly, the specimen shows a thick bony boss dorsal to the most anterior palatal tuberosities (Figure 3c). Details of the surface of this dorsal boss were lost by weathering; therefore it is not possible to identify the parts of the anterior end of the braincase, but there is little doubt that they were connected in some way in life. Its anterior end of the boss must have supported the base of the internasal septum as it does in dipnorhynchids.

The dorsal surface of the posterior third of the pterygoids is difficult to interpret. The bone must have been particularly coarsely grained and thick, and much of it has been eroded away during preservation. The lateral margins have a high rounded ridge, best preserved on the left side (Figures 3b,c), and these presumably surfaced in a weak dorsal palatal process. This area is weathered on both sides of the specimen, but the bony trabeculae preserved suggest that such a palatal process was present. The contours of the surrounding bone indicate that the process was unlikely to be as strong as the ones in dipnorhynchids. Behind that the surface drops away to what must have been the quadrate surface. As mentioned above, no strong ossified wall supporting

the otic region of the braincase is preserved. This region must originally have been made of cartilage.

The postero-central part of the visceral surface forms a high ridge (Figure 3c) which is smooth crested and is supported by very coarsely vesicular underlying bone. The median part contains a well rounded perforation for the buccohypophyseal stalk (Figure 3b), but the stalk does not continue down to the palate. We note that in *Dipnorhynchus*, we have a single specimen in which no buccohypophyseal opening is present, even though all other specimens have such a structure. During periods of regrowth, the surface of the palate was covered by hard tissue and the buccohypophyseal opening was at least temporarily covered.

In neither ventral, dorsal nor posterior views does the bone structure show evidence of sutures between what could be regarded as a boundary between the parasphenoidal bone and the pterygoids. So far as we are aware the parasphenoid boundary in this region remains unknown. This matter will be dealt with separately in the latter part of the paper. At this point we note that sections across a well preserved palate of *Dipnorhynchus kurikae* show no evidence of any boundaries of a parasphenoid on the buccal surface, and new specimens of *D. sussmilchi* (Campbell *et al.* 2000) confirm this view. The dorsal view of another specimen of *D. kurikae* shows an edge which we presume is the margin of the parasphenoid extending forwards around the anterior edge of the buccohypophyseal opening. In *Dipnorhynchus*, therefore, the parasphenoid does not appear between the dental plates on the palatal surface, but probably continues forward on the visceral surface to the buccohypophyseal canal.

In *Dipnorhynchus* the antorbital wall and the postnasal process are large and heavily ossified, forming a distinct feature in dorsal view. We note that there is no evidence of such a feature in *Dipnotuberculus*, even though our specimen is relatively well preserved in these areas. Presumably the posterior wall of the nasal cavity and the antorbital wall were made of cartilage.

Mandible External Surface

The specimen NMS 1993.57.1 is the only individual available that shows the external bones of the mandible, and it is incomplete (Figure 2a-c). Most of the external surface is covered with cosmine, though there is a break in this substance against the dentary. This specimen was broken during transport and the photographs of the entire specimen were made by Dr Lelièvre. We also have colour photographs made by Smithson. Campbell has examined the broken specimen in Edinburgh and has photographs made by Ms Susan Stevenson from the National Museum. of Scotland. Some of these are used herein.

The mandible is wide in comparison with its length (reconstruction Figure 4), even more so than *Dipnorhynchus*. This accords with the width of the palate described above. The dentary is wide and short, but it does not extend posteriorly to make a sharp boundary to the anterior furrow as it does in *Dipnorhynchus*. As a result, the dorsolateral posterior end of the dentary is much shorter than that of the dipnorhynchids. In lateral view the posterior end of the dentary turns ventrally to make a ridge across the posterior end of the labial pit (Figure 2d). Such a structure is not present in *Dipnorhynchus*, in which the dentary forms a straight dorsal edge to the labial pit (Campbell and Barwick, 1985, figures 8c; 9b). The surface of the dentary carries perforations much coarser than the cosmine pits as is normal for dipnorhynchids (Figure 2d).

Posterior to the dentary on the buccal surface is an anterior furrow, much of the floor of which has been broken away. Medially in the anterior furrow is a low rounded elevation in the floor with a rounded top, which does not reach to the height of the dorsal surface of the dentary. A similar ridge is developed to a variable extent within a single species of some dipnorhynchids. The floor of the anterior furrow carries foramina which open down into the mass of symphyseal tubules (Figure 2c). The two preserved foramina are not symmetrically placed with respect to the mid-line. Other foramina must have been present, but the basal bone is not preserved in the lateral parts of the furrow.

The end of the dentary lies opposite a depression in the sides of the prearticulars lateral to the large anterior tubercle (Figure 2a). This gives the prearticular a distinctive outline. Another foramen lies in this furrow posterior to the dentary (labelled *pit* in Figure 4a), and this is the homologue of the foramen found in *Dipnorhynchus sussmilchi*; it probably opened ventrally into the Meckelian cavity.

The labial pits are not well preserved, but the broken specimen NMS 1993.57.1 shows some interesting features (Figure 2d). Ventrally the pit is surrounded by the surangular, and anteriorly and dorsally by the dentary. At least part of its inner surface is covered by the Meckelian bone. These features are common in the dipnorhynchids (Thomson and Campbell, 1971; Campbell and Barwick, 1999, 2000).

The mandible is long medially (Figure 2a,b), but the arrangement of the prearticulars and the external dermal bones in the mid-line are different from those of *Dipnorhynchus*, which has a similar length. In *Dipnotuberculus* the join in the prearticulars carrying the dental plates drops ventrally near the posterior end of the first lateral tuberosities (Figure 2a; 5a), and the posterior floor of the lingual cavity is made up of a thin covering

of prearticular bones lying on the external dermal bones (Figure 2 a,b). In *Dipnorhynchus* the dental plates on the prearticulars are much longer medially, and they drop ventrally almost over the posterior end of the splenials making a sharp vertical wall posteriorly.

Four infradentaries are present, as is normal in *Dipnorhynchus* (Figures 2b; 4b). The sutures between the bones are restricted to the posterior part of the surface, and the anterior parts are covered with cosmine. So far as can be observed, the surangular is a narrow bone and its anterior edge runs forwards beneath the labial pit (Figure 2d), a point which can be seen on the broken specimen. It carries a large number of perforations especially towards the anterior end (Figure 2d), indicating that the lateral line canal continues this far forwards. Although its outline is not clear because of cosmine cover, the angular is probably a triangular bone which stops short of the anterior end of the surangular. It carries a large number of perforations which indicates that the lateral line runs obliquely forwards to connect with the transverse commissure, the exact position of which is not clear. The splenial is narrower than the postsplenial, which is narrower than the angular.

Mandible Buccal Surface

This is preserved on two specimens NSM 1993.57.1 and UALVP 44559. Most of the surface is covered by large prearticular plates that join medially, and have no median suture separating them (Figures 2a; 5a). The lateral walls of the lingual cavity are formed of the prearticulars which stand as a vertical wall (Figures 2e; 5a,c), and the posterior end of the lingual cavity is floored by a thin layer of prearticular against the dermal bones.

The dental plates are thick and make a hard buccal surface. The histology of the plates is discussed below. The lateral margins of the prearticulars are formed of three elongate, large rounded tuberosities that stand up higher than the more mesial surface (Figures 2a; 5a). These tuberosities are not bounded by a more lateral ridge. In dorsal view the dental surface has a deep lateral embayment lying opposite the posterior projection of the dentary, another one between the first two lateral tuberosities, and a third deep embayment for the adductor pit (Figures 2a; 5a). This gives the lateral margin a distinctly waved edge. The most anterior lateral tuberosity is the largest one present, and extends forwards almost to the anterior end of the dental plate. The second tuberosity is shorter and its long axis is slightly anterolaterally directed. The third tuberosity is very much shorter, and it does not have a distinct long axis. The tubercles are separated by deep grooves, on the mesial sides of which are rough-based depressions. In addition there is a smaller cavity

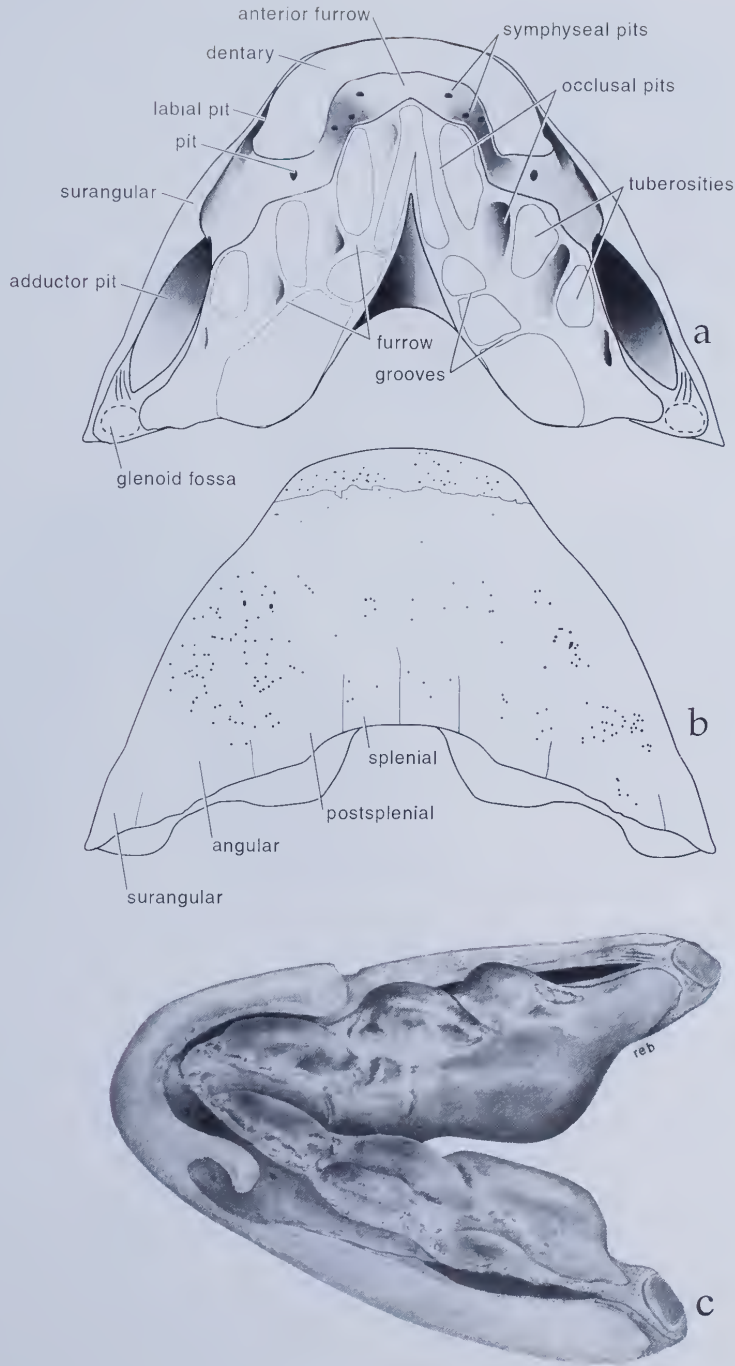


Figure 4 (a–b). Reconstructions of the dorsal and ventral outlines of NSM 1993.57.1. (a) is a composite figure which includes information from the holotype, because the surfaces of 1993.57.1 are not clear in places. (b) is drawn symmetrically from all the data available. (c) Three dimensional structures of the specimen NSM 1957.57.1, showing the form of the lingual furrow, the anterior furrow, the adductor cavity and the position of the main dermal bones.

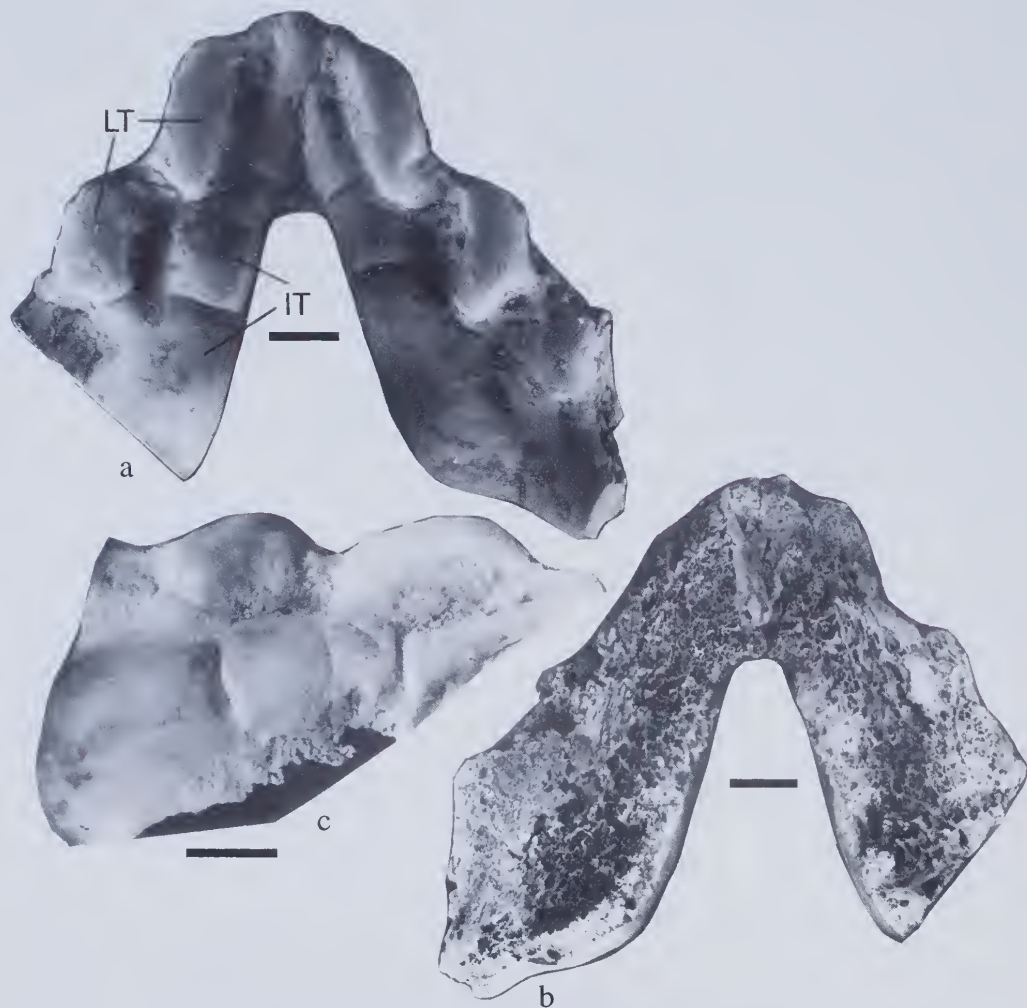


Figure 5 The holotype of *Dipnotuberculus gnathodus* gen. et sp. nov. UALVP 44559 (a–b). Dorsal and ventral views of an incomplete mandible. Note the large lateral tuberosities (LT), the spaces into which the palatal tuberosities occlude, and the divided internal tuberosities (IT) and the gaps between them. (c). Lingual view of the dental plate and the broken tissue bordering it. Note the rough surface marking the occlusal surfaces. Compare it with Figure 2e.

behind the posterior tuberosity and adjacent to the adductor pit, into which the anterior end of the posterolateral ridge on the pterygoid must have occluded (Figures 4a; 5a). These depressions mark the surfaces where the tuberosities of the mandible occlude outside the main line of the tuberosities of the palate. The long axes of the depressions are directed anteriorly, and their surfaces are irregular, because the dentine of the plate is interrupted by the calcite of the matrix being so close to the surface (Figures 5 a,c; 8 b,c).

Medial to the lateral tuberosities and the above depressions, is a dorsally rounded ridge which

medially drops vertically down into the lingual cavity. Anteriorly this ridge extends forwards to the anterior end of the dental surface, becoming much narrower as it goes (Figure 5a). The buccal surface of the ridge is broken up into large rounded tuberosities separated by thin grooves. These bands do not match on opposite sides of the one specimen. On UALVP 44559, the left side has two grooves, the posterior one being medial to the posterior end of the second lateral tuberosities. The right side has this groove further forward. Both sides have a small oblique groove running anteromedially from the posterior end of the anterior tuberosities. NMS

1993.57.1 has a different mode of subdivision of the ridge as is shown on Figure 2a,e. These grooves are matched by the small grooves which separate the lateral tubercles from the inner rounded tubercles.

The margins of the dental plates indicate how these were modified during growth. The lateral margins show small blisters which are isolated like those of the palate (Figure 3d). The structure of the lingual surface of the dental plates is shown on UALVP 44559. These indicate that the mode of lateral growth was the same in each jaw. The structure of the dental plate margin along the lingual furrow is well shown on both mandibles. In the lingual groove of UALVP 44559, the continuous layer of dental material has a sharp boundary and below this the surface is made up of blisters of different material (Figure 5c). These blisters are separate from one another and show sharp lines at their boundaries. Some of them also lie in resorbed patches at the edge of the continuous dental surface. Clearly they are replacement structures on the inner edge. On NMS 1993.57.1 (Figure 2e), the edge is made of sharp projections, presumably the remnants of a resorption further advanced than in the other specimen.

A large adductor foramen, with a pointed anterior end and a bluntly rounded posterior end, reaches to about half the length of the mandible. Its pattern is similar to that of *dipnorhynchids*. Anterior to the adductor fossa, the prearticular almost certainly extended laterally to join the surangular, but in the specimen this junction was broken during preservation (Figure 4a,c).

The specimen NMS 1993.57.1 has part of the glenoid fossa preserved. By restoring the preserved edge of the surangular to the prearticular it is possible to estimate the size of the articulation (Figures 2a; 4a,c). For a jaw of this size, the fossa is unusually small when compared with that of *Dipnorhynchus*. However we note that although we do not have a quadrate preserved, the structure of the palate also indicates that the quadrate process must have been small. This fits in with the conclusions about the fossa in the mandible.

The preglenoid area in NMS 1993.57.1 has been broken through, but it is clear that the articular was not a large bone, and the preglenoid process was not high. Part of the preglenoid process is preserved and shows a linear arrangement (Figures 2a; 4a,c) suggestive of muscle attachment such as occurs on *Dipnorhynchus kurikae* (Campbell and Barwick, 2000). This was interpreted as a muscle or ligament attachment which served to stabilise the glenoid region during biting.

Mandible Internal Space

The internal space of the mandible is largely open, but it is too poorly preserved to see the detail one sees on *dipnorhynchids*. The inner surface of the

dentary and the anterior part of the surangular are covered with a dense mass of symphyseal tubules (Figure 2c). These extend beneath the labial pit. Some of the canals descending into these from the anterior furrow are still visible on the right side of the specimen.

On the prearticular a strong ridge lies beneath the lateral row of dental tuberosities, and this makes a sharp edge against the Meckelian bone (Figures 2f; 5b). A similar ridge occurs in *Dipnorhynchus*, but it is not as large as the one in *Dipnotuberculus*.

The left side of the broken NMS 1993.57.1 specimen shows the remains of a thick ossified Meckel's cartilage exposed along the posteromedial wall (Figure 2f). Within it there are foramina, but the region lateral to these foramina is broken away, and so the exit of the ramus mandibularis nerve N V is not preserved. The preserved foramina have not been identified. The Meckelian bone runs up inside the prearticular and shows a parallel striped surface with many foramina. This surface is comparable with the Meckelian bone lining the prearticular of *Dipnorhynchus cathlesae* (Campbell and Barwick, 1999, figures 11A,C; 12D; 14A). The surface of the bone has the appearance of stress lines. *Dipnorhynchus* has multiple vertical rugae along the inner face of the Meckelian bone (Thomson and Campbell, 1971, figures 47–48), these having provided expanded surfaces for the attachment of the adductor muscles. No such rugae have been found in *Dipnotuberculus*.

GROSS FEATURES OF THE DENTAL PLATES

The buccal surface of the palate shows little or no sign of wear due to abrasion, except in the grooves into which the tuberosities of the palate occlude with the prearticulars. If the surface had been worn during life, many more surface features would have been removed. Not only would the marginal tuberosities have been worn down, the rounded tuberosities in the medial part of the mandible and the large flatted tubercles on the palate, would have been reduced. In addition, the grooves in the surface are clearly outlined. Consequently we conclude that the surface of the dental plates must have been remoulded during life. The question now is how could this have taken place?

In the following text we make a distinction between the broad rounded **furrows** separating the lateral tuberosities from one another and the lateral tuberosities from the more median tuberosities on the one hand, and the finer **grooves** which occasionally lie in the above depressions, or separate tubercles as on the inner tubercular ridge on the mandible (Figure 4a). On the palate the median tuberosities are separated from the flattish tuberosities on each side by similar furrows. In addition there are much finer depressions or

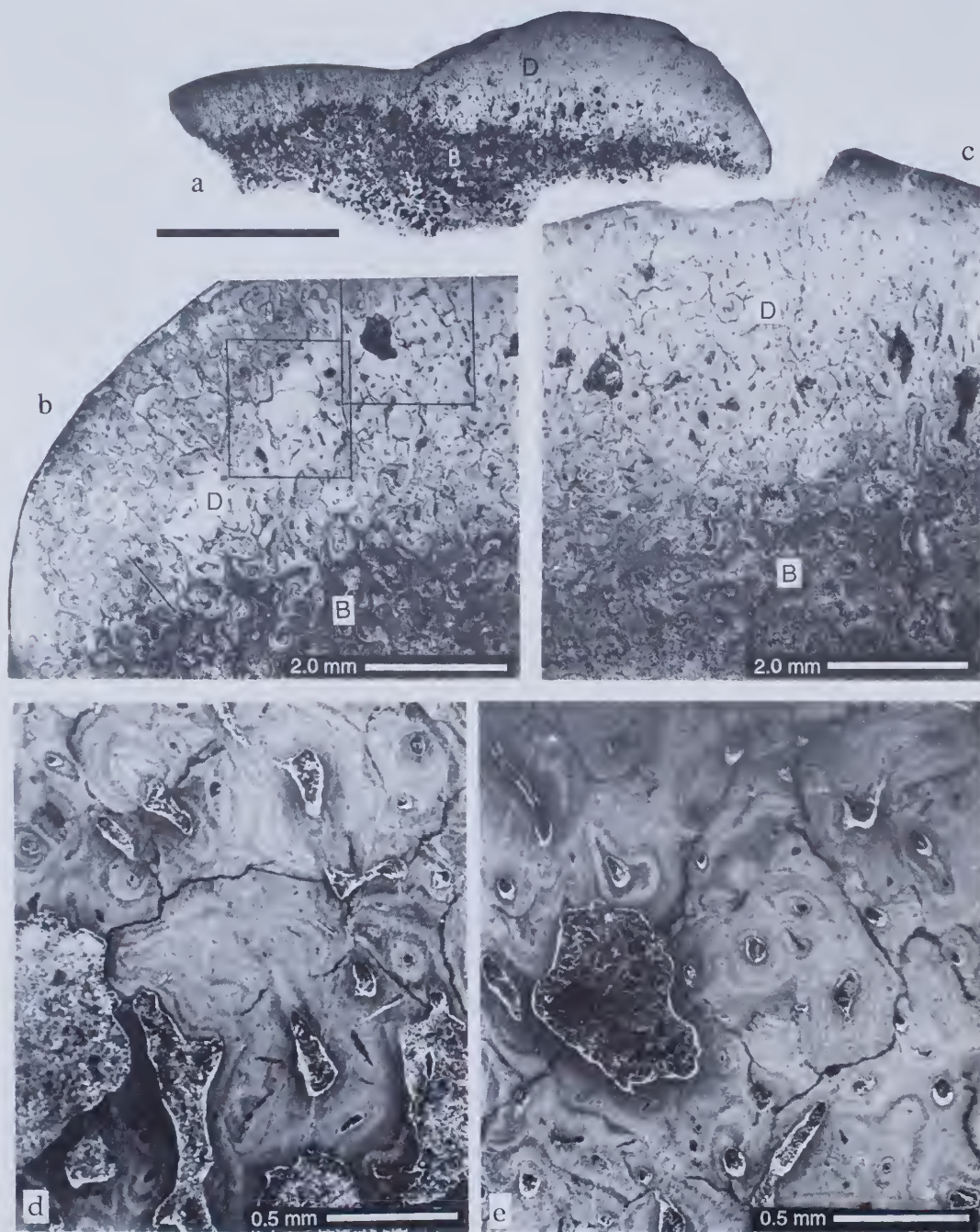


Figure 6 Vertical sections across the dental plate of the holotype, cut from the posterolateral corner of the specimen. (a). Print from a thin section with the lateral tuberosity to the left. The thick tissue to the right is the large internal tuberosity. Note the large perforations in the lower layers of the dentine and the clear boundary between the bone (B) and the dentine (D). (b–c). SEM images of a section cut parallel with the slide in (a); lingual furrow to the left, that is the section is in the reverse orientation to (a). Bone at the base marked (B) and the transition into dentine (D) dorsally, clearly marked. Note perforations in the dentine and the clusters of dentine with irregular boundaries around one or more vascular bundles. The relative positions of the two images is indicated by the small resorbed space at the upper right hand side. (d–e) SEM images of the points marked on (b) showing resorption boundaries around clusters of vascular bundles.

grooves which in places lie in the furrows between the lateral tuberosities and extend medially to separate other tuberosities. On the mandible, similar grooves occur on the medial edges of some lateral tubercles, and they also divide the long medial tuberosity into the irregular subdivisions we observe. In the furrows the dentine is thin and the bone approaches the buccal surface, a feature that will be described below. This allows new dentine and new bone to be added at these furrows, and the dental plates are expanded. The lateral tubercles are evenly spaced and their position is determined because they have to occlude with the tubercles on the opposing jaw. Along the medial elongate tuberosity, the tubercles are not involved with precise occlusion and their position is the result of renewal processes along the ridge. New material would have been added at the grooves, and it would not have to be regularly spaced.

Periodic growth has been described from *Dipnorhynchus* (Campbell and Barwick, 1999, 2000). Such a phenomenon would have been difficult to explain if thick dentine was the material forming the dental plates as is found on Late Devonian and later genera. In *Dipnorhynchus* the pterygoids and prearticulars are thick, and part of their surface is covered with a thin sheet of dentine which varies in thickness according to its position on the dental plates. The surface of the dental plates have been

modified by differential rates of growth in the underlying bone. The dentine is also modified by growth at the contact between the dentine and bone, and the shape of the dental surface is modified by periodic outgrowths of new bone via growth at the base of the superficial material.

The dark-coloured dental tissue in *Dipnotuberculus*, which is determined below as a distinctive form of dentine, forms a layer up to 9+mm in thickness in the main posterior tubercle (Figure 6a), but slightly thinner in the lateral tubercles. No evidence of a thin layer of hard material occurs on the buccal surface of this dark coloured layer, but the entire layer is made up of the same material. The dentine is densest towards the buccal surface, but becomes more open ventrally towards the bone of the prearticulars. The contact between these two tissues is discussed below, but it is clear that the dentine is added to by the formation of new tissue at the junction, and by resorption and deposition of pleromic dentine in the resorbed spaces. This allows the dentine to be remodelled by internal processes. The details of this process will be discussed below.

This explains how the thickness of the dental plate material of the palate increases, but it does not explain the lateral extension of the plates and the marginal tubercles. The lateral extension of the palate could take place by additions at the posterior



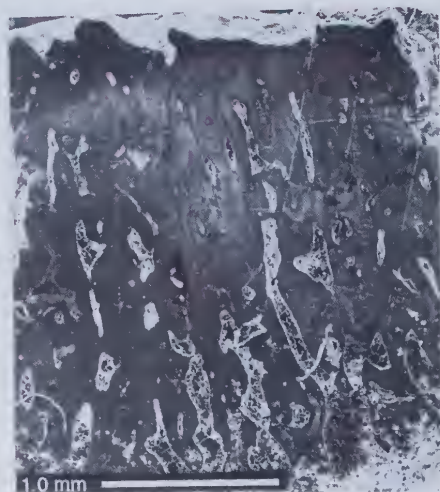
Figure 7 Drawings of parts of Figures 6 d–e, large open resorbed areas in black showing marginal resorption, cutting into the growth lines marked as dotted lines. Vascular bundles also in black and are surrounded by dotted lines showing the layers of concentric tissue. The boundaries of former resorbed areas, now occupied by pleromic dentine, are shown by dark lines. Note that the first layers extend around the whole resorbed area and successive layers are around vascular bundles. Not all layers are represented, but only those which show the main features.

and lateral extremities. This would require no additions to the pterygoids internally such as occurred by the addition at a median suture in most later genera. We do not suggest that all addition would take place at the posterior and posterolateral edges, but this was the main area of addition. Such a suggestion is completely different from extant species of dipnoans. But we do have a specimen of *Dipnorhynchus sussmilchi* where the early stages of growth show the lateral margins anteriorly, and new marginal ridges were being added to them at their posterolateral ends (Campbell and Barwick, 2000).

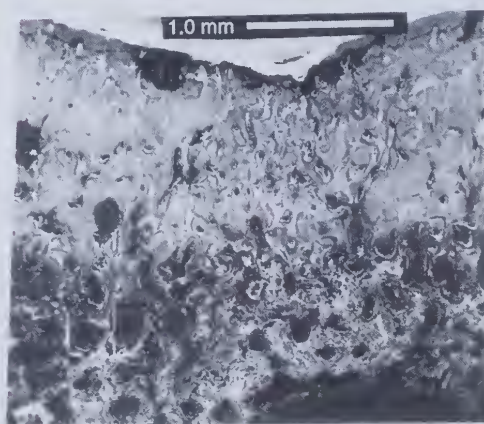
Small scale lateral addition took place on already existing tuberosities and anterolateral margins by small rounded blisters lying on the surface. These were often obliterated by erosion during preservation, but in other places they are clearly preserved (Figure 3d). Such an arrangement has been observed in *Dipnorhynchus* (Thomson and Campbell, 1971, figures 79–80) and in *Chirodipterus* (Smith and Campbell 1987, figures 27–31). In *Dipnorhynchus* the composition of the blisters has not been investigated by thin sections, but they are probably made of dentine. In *C. australis* they are made of dentine. Lateral growth of the dental plates of both species would have occurred while the epithelium covering the plate margin permitted the plate to incorporate the blisters. Presumably a similar process occurred in *Dipnotuberculus*.

HISTOLOGY OF THE DENTAL PLATES

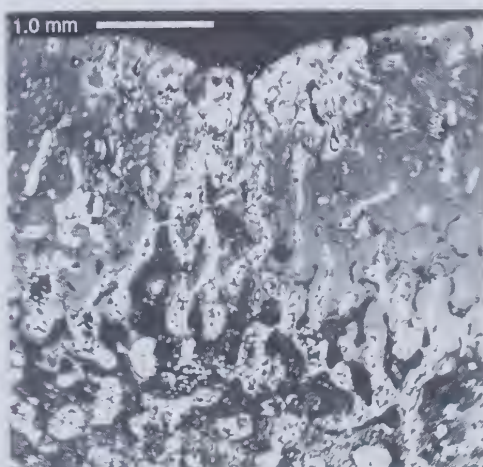
The posterior end of the left ramus of the mandible UALVP 44559 was broken across, and the details of the bone and dental plate structure could be observed (Figure 6); sections show that the bone was bored by fine organisms, probably fungi, after death. A thin section and two SEMs were prepared of this specimen, and they are figured on Figures 7–10. Note that all the sections examined for this work have been cut parallel with each other, and occupy the posterior end of the prearticular. We would have preferred to have sections cut in a variety of directions, but we have insufficient material to do this. Although the genus is not the most primitive of all those known from the Dipnorhynchina, it provides the best example of the histological detail



a



b



c

Figure 8 (a) SEM image of part of a lateral tuberosity cut so as to show the long thin openings for vascular tissues. (b–c). Two SEM images of the contact between the outer and inner tuberosities. (b) shows a boundary between the lateral and median tubercles, the bone approaching the buccal surface. (c) is close to the occlusal space for the upper tubercle and shows calcite filled cavities almost to the buccal surface.

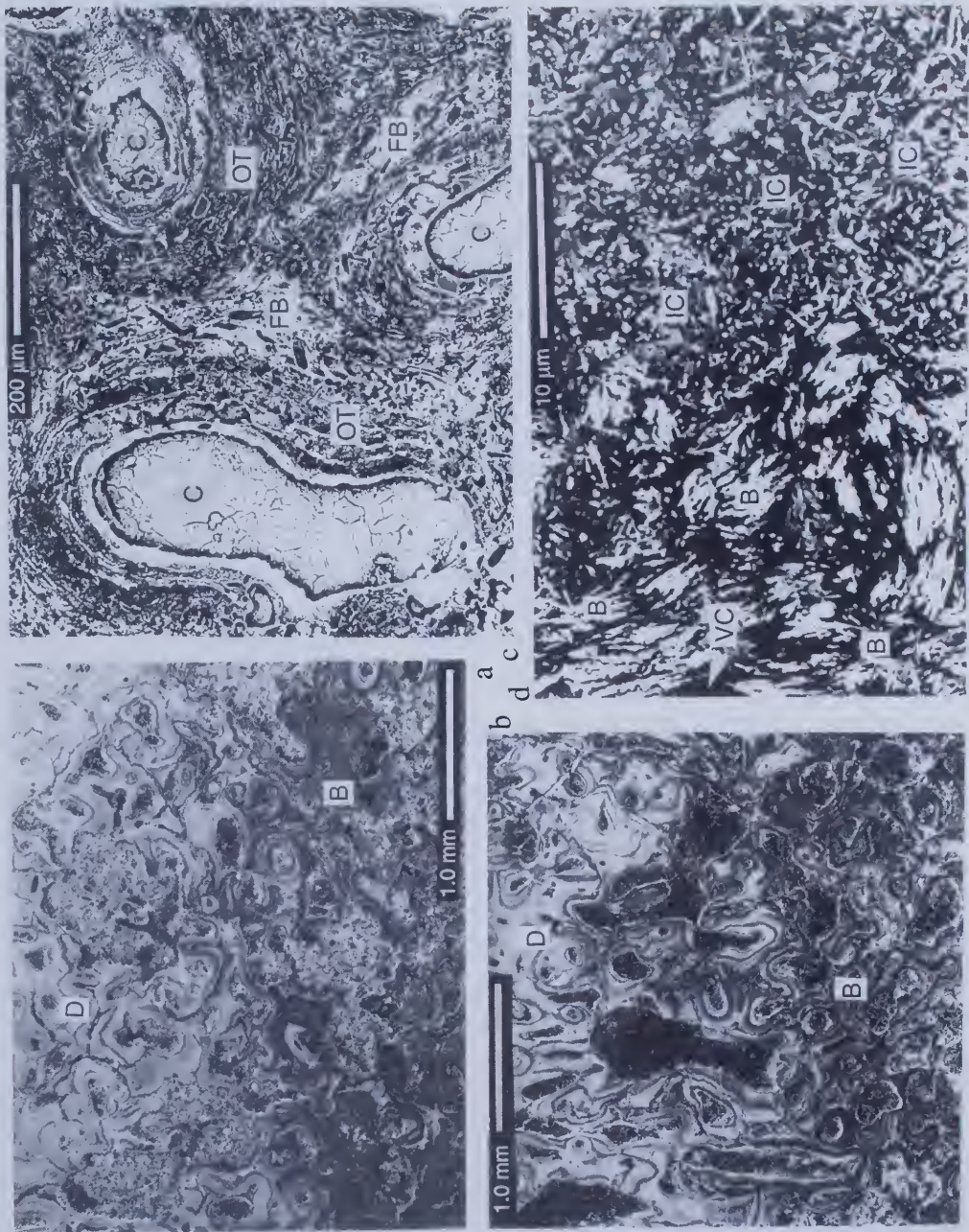


Figure 9 Landscape image of back scatter SEM images from the holotype. On all images the buccal surface is to the left side of the plate. (a). Section through the contact between the bone at the base (B) and dentine (D) at the top, with the transition between the two types of tissue shown up by the growth of later tissue around the vascular canals and sediment between the vascular units. (b). Similar section to (a) with layers of tissues well defined. (D) is dentine and (B) is bone. Reversal lines clearly shown. (c) Detail in the bony tissue with calcite-filled vascular canals (C), surrounded by concentric layers of ossified tissue (OT) and separated by layers of relatively unossified tissue containing numbers of fungal borings (FB). (d). Section through the dentine with the edge of a vascular canal (VC) on the left margin bordered by a layer of crystal bundles of apatite (B) and by irregularly arranged apatite crystals (IC). Note the elongate crystals more or less parallel with the surface and white spots representing end views of crystals.

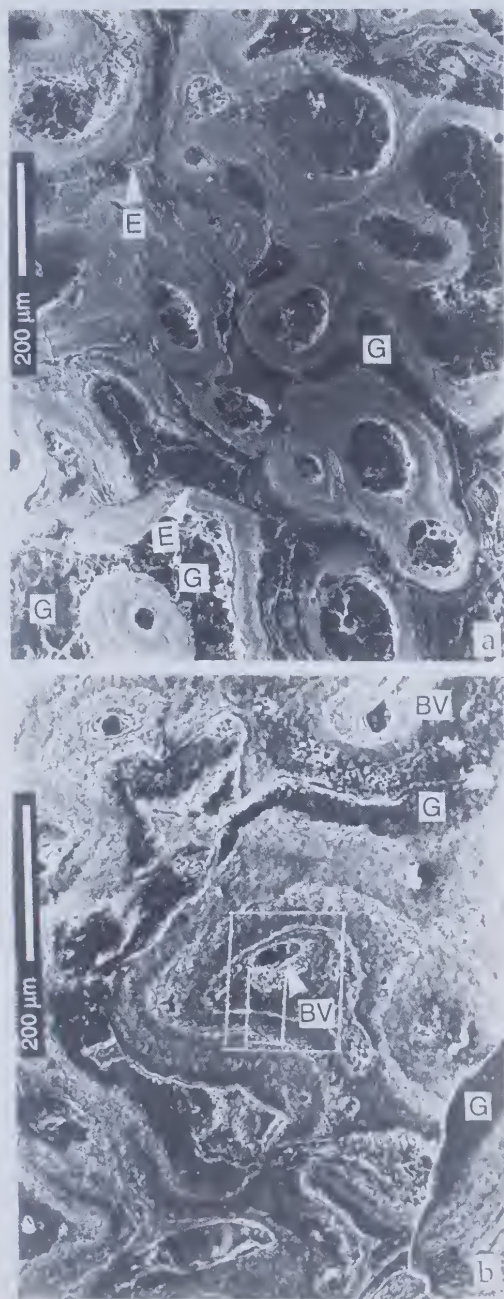


Figure 10 Back Scatter SEM images of two sections of dentine (a). Dentine near the contact between the bone and dentine. Resorbed edges shown (E) and obvious gaps (G) which were originally occupied by soft tissue between the dentine bundles. (b). Near the contact between the bone and the dentine showing calcite filled spaces within the vascular openings and the spaces between the vascular bundles (BV). Gaps and resorbed edges as in (a). Area outlined is reproduced at greater enlargements in Figures 11a,b.

of that group available. The Australian specimens of *Dipnorhynchus* are heavily modified by boring and perhaps slight recrystallisation. On one specimen of *D. sussmilchi*, ANU 18815, a small patch of palatal dentine shows dentine tubules arising from the thin vascular columns. Campbell and Barwick (1999, 2000) have illustrated some of the tissue which seemingly is without dentine tubules.

In much current terminology, the presence of dentine tubules is regarded as an obligatory character of dentine, but this is not correct. Naturally in this investigation we were interested in discovering if dentine was present, and for this reason the discovery of dentine tubules was an objective. Nowhere in any section examined by SEM or by optical sections were such tubules found (Figures 6–12). In the absence of tubules, dentine can be distinguished by its position in relation to bone and the depositional surface, by its lack of spaces that could be interpreted as osteocyte spaces, and by the clear crystalline nature of the tissue discussed. In *Dipnotuberculus* the dark-coloured material lies between the lamellar bone with its osteocyte spaces and the surface of the dental plates, although no enamel has been discovered on the plates. Thus this tissue has the position of dentine, and is crystalline, but it lacks osteocyte spaces and dentine tubules. We therefore refer to it as dentine. Note however that in some sections it contains numbers of open spaces (Figure 11c), that could be interpreted as sections across tubules, but these show no sign of being organised into a linear pattern. This could be the result of the orientation of the section, though this is unlikely. Also the margins of vascular canals show no sign of tubules around them, places where they should appear if they were present, because no infilling had taken place. In our view no dentine tubules are present in *Dipnotuberculus*.

The dentine lies directly on light coloured bone, and the contact between two tissues is continuous. No sign of a pulp cavity is present. Optical sections expose depressed osteocyte spaces in the bone, which are depressed in vertical section, but are more obvious in horizontal sections. As Figure 9c shows, distinct osteones contain laminar bone in which the osteocyte spaces have been observed. Between adjacent osteones there are lightly mineralised cancellous tissues (Figure 9c), or spaces which are now filled with calcite. In the contact areas where the lateral tuberosities meet the larger median tuberosities (Figure 8b–c), the bone comes close to the buccal surface and spaces within it are

occupied by sediment which in places continues through the overlying dentine to reach the surface.

Towards the contact with the adjacent dentine, the white bone has darker layers within it, and these are closely similar to the nearby dentine (Figure 9a,b), and they contain no osteocyte spaces. In some places the laminar bone alternates with the dark-coloured dentine, indicating that a change took place from deposition of bone to dentine more than once. This seems to be a very complex pattern and may be called into question, but we see no other interpretation of our observations. Analysis of the dark layers using the EDAX method on the Cambridge SEM did not show any chemical difference between these layers and the dentine. This suggests that both osteocytes and odontoblasts occurred in the vascular spaces, and the different hard tissues were deposited alternately. As a result of this there is a gradation between bone and dentine over a short vertical distance, but the change is sufficiently rapid to produce a clearly defined boundary to the naked eye.

Sections through the dentine of both the lateral and more median tuberosities are illustrated. The dentine close to the bone contains a number of open spaces now filled with calcite (Figure 10a,b), which represent soft tissue spaces in the original. In addition some large spaces show that they were resorbed from the surrounding dentine, and their edges are reversal lines (Figures 6b–c; 12c,d). Their boundaries cut across the concentric bands of the adjacent tissues. The number of such openings decreases rapidly towards the buccal surface. Some of these openings are irregular in shape, but others are long and narrow, the elongate ones being long sections of vascular canals and show concentric banding around their margins (Figures 6d; 12c,d).

We conclude that large resorbed openings were subsequently filled by new dentine deposited around newly formed arborescent pulp canals. In the sense of Campbell and Smith (1987), this infilling dentine is an example of pleromic dentine. In many places, the infillings are lined with extensive bands of dentine which must have been deposited by odontoblast cells lining the inner surface. These layers surround several smaller vascular canals which occupy the main body of the space. There are branches of these canals showing that they were arborescent in their form. Each canal is surrounded by concentric layers of tissue, demonstrating that the layers were deposited in succession around the canals. Ultimately the whole resorption space was filled with dentine, and many of the smaller vascular canals were almost completely occupied by dentine (Figures 6d,e; 7a,b; 12c,d; 13a,b). In some other areas a single vascular canal occupies a whole resorption space (Figure 13).

Sections through the dentine in the lateral and the large internal tuberosities are illustrated in several figures (Figures 6b,d,e; 9d; 11a,b). The vascular canals in the surface layers are variously oriented, but some are almost at right angles to the surface (Figure 6b,c). Others have random orientation, and are closely spaced. Towards the base of the dentine near its contact with the underlying bone, they are more widely spaced than near the buccal surface, and the spaces within the columns are largely open. Towards the buccal surface they are densely packed, have small open spaces within the columns, and the columns are packed one on the other.

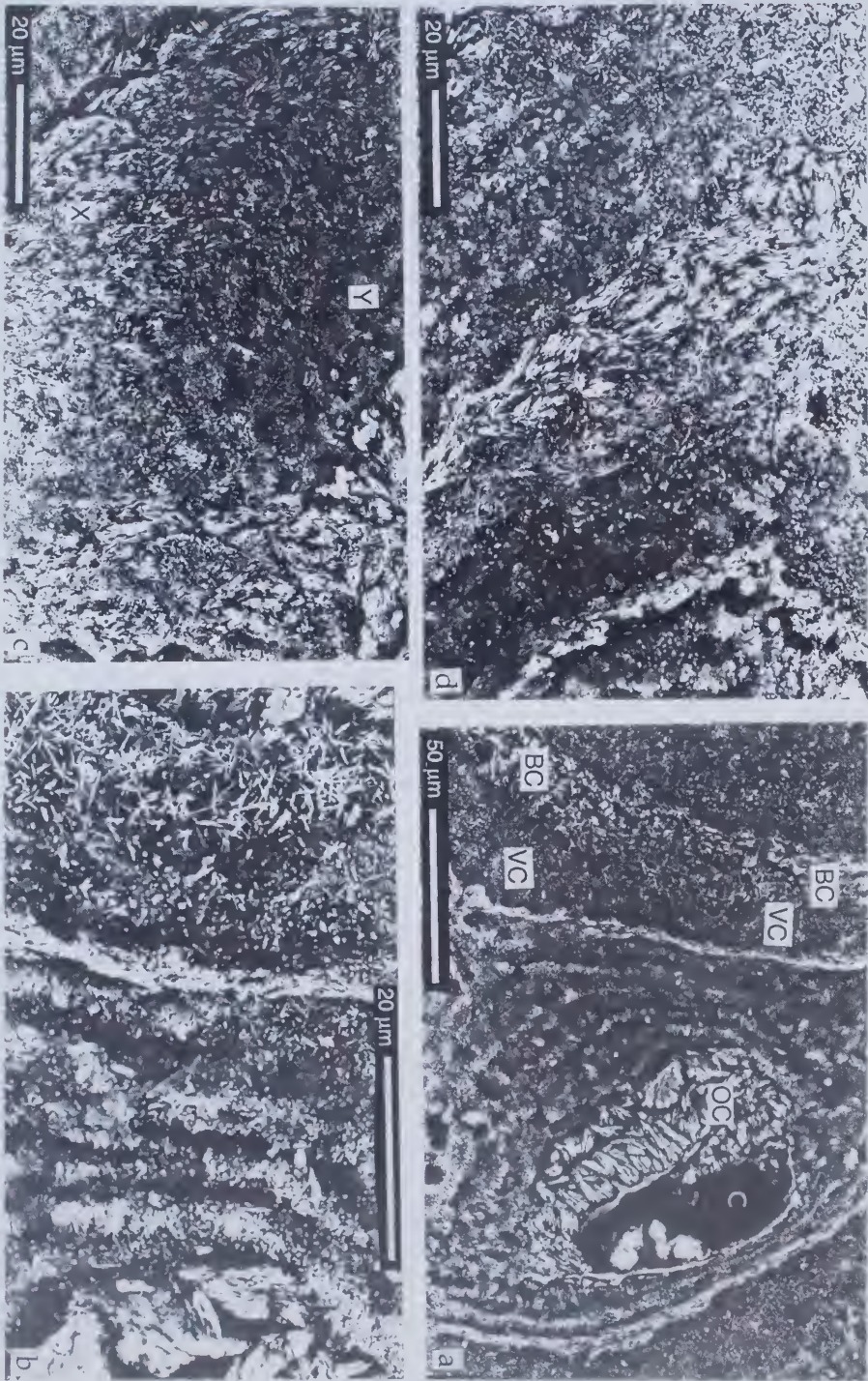
The dentine has been examined in optical thin sections and by SEM examination of sections cut parallel with the optical section. The layers of tissue are continuous and indicate that they were laid down in columns around the vascular canals. Obviously, as the soft tissue retreated down the canals during growth, it left behind the successive layers of tissue. So the next question is what causes the light and dark banding? EDAX shows that there is no difference in chemistry between the layers. However, enlargement by SEM shows that the layers have different crystal patterns. Some layers have crystals in bundles in a variety of orientations in relation to the boundary of the layers, alternating with layers of randomly oriented crystals some crystals oriented normal to others (Figures 11a–d; 13a,b). In most instances the boundaries between the layers are clear, but elsewhere there is a gradation. In some places it is possible to recognise separate layers within a single coloured band of tissue (Figure 11b). This implies periodic deposition of a single layer. No evidence of osteocytes is found anywhere in this hard tissue.

The pattern we have described produces a structure described by Ørvig (1951: 335) as dental osteons. Ørvig goes on to comment that 'the lamellae contain delicate fibres which alter their directions somewhat from one lamella to the next'. Assuming that the orientation of the cells controls the orientation of the crystals, such an observation would provide an explanation of the data given above. However because the overall structure is complicated into multiple groups of vascular canals, the structure in *Dipnotuberculus* is more complex than this. The hardness of the buccal surface was probably increased by the alternating layers of crystal bundles.

GROWTH OF THE DENTAL SURFACES

No growth series of the dental plates is available, but it is possible to give some indication of how the plates grew.

1. There is no enamel on the surface of the plates as they are preserved, and the dentine in the structure is different from that of any dipnoan



such as the extant species, as well as any Late Devonian or Carboniferous species.

2. The growth of the lateral tubercles and of the surfaces of the tissue inside them implies that the growth during the later ontogeny took place by the addition to the base of the plate which permits the thickness and the lateral extension of the elements to occur. The palatal material thins out at certain points and the underlying bone becomes close to the buccal surface laterally, allowing extension to occur. This allows the dentine of the plate to replace bone laterally as well as vertically, although the vertical growth is at a greater rate than the lateral growth to maintain the rounded structure on the features of the buccal surface. For this process to take place, there is obviously no need to have a space at the base of the dentine, but rather larger canals in the base of the dentine, which are progressively filled up with new tissue.
3. Another method of adding to the margins of the tooth plates is by the addition of blisters on the sides of the plate. Similar features occur in *Dipnorhynchus* and *Chirodipterus australis*. In this new species the bone of the prearticular and the pterygoid grew laterally into the spaces between the blisters and joined them together.
4. The growth of dentine at its base must require a change in the material deposited. This does not result from the replacement of prearticular or the pterygoid bone, but by a change in the material deposited in the vascular spaces to form complete layers of new material. This produces the dense mass of dentine in the plate. Because the growth of the plate continued through the ontogeny of the animal, one would expect to find some lighter coloured layers in the tissue towards the buccal surface resulting from deposition when the animal was young.
5. Finally, the spaces into which the tuberosities of the palate fit into the prearticulars, show a coarse texture resulting from the intergrowth of the basal bone and the dentine. As indicated above, this allows differential growth to take place.

The lateral tuberosities were present early in the

growth of the animal, and were added to vertically by growth into the basal bone and laterally into the open labial space. Their inner edges are moved laterally as new material is added at their inner margins. Growth of bone took place in the furrows causing extension of the plate laterally, but not producing any obvious sutures. This is shown on Figure 8 b, c. The structure of the palate is not so clear as we had hoped, and we are unable to cut it for thin sections. However, there are features that support the view developed from the mandible. The tuberosities are large and smooth surfaced, indicating that they have continuous accretion of dentine and bone beneath them. The furrows in between are much rougher on the buccal surface, indicating that they are made of a mixture of hard dark bone and pterygoid bone. Thus the bone must be close up under the buccal surface, a feature which we would expect if our mandibular interpretation is correct.

With regard to the palate, no median suture is present, so that the growth of the plate had to take place along the lateral and posterior margins. In dentine plated forms the median edge is a zone of active modification as the tissue was eroded and added to periodically. This also means that there would be no addition of tissue to the lateral margins of the parasphenoid. That bone could increase only by addition to its posterior and posterolateral edges. Where the anterior edge of the bone lay is quite unknown. In later dipnoans, the buccohypophyseal opening is near the anterior end of the parasphenoid. As a result, we would expect the edge to be in about that position on our current specimens. In the light of what we have written about the addition of tissue to the palatal surface, care has to be taken about the use of furrows in the surface to define the boundary of the bone. We also note that the absence of a buccohypophyseal foramen in one specimen may be the result of deposition of the tissue of the dental plates over its surface in later life.

In the mandible, the dental plates also have a number of replacement patches low on the lingual surface and apparently made of the same material as the dental plates themselves. We suspect that it forms a means of modification of the inner edge of

◀ Figure 11 Landscape image of back scatter SEM images of the dentine making up the large tuberosities. Buccal surfaces to the left side of the Figure. (a) An asymmetrical section, being an enlargement of Fig. 10 b. Bundles of crystals against the vascular canal (C) followed outwards by layers of organised crystal bundles alternating with irregularly arranged fine crystals. Larger layer of organised crystals (OC) and then wider bands of crystals at right angles to the surface (VC) and a layer of bundled crystals (BC). (b) An enlargement of part of (a). Note that in the banded section on the right of the image most of the crystals stand with their axes at a high angle to the surface, but the orientation of the crystals in the dark bands is not known. (c-d) Two further views of the several layers showing crystal orientation. Note in (c) that the character of a single layer of crystals may change along the length of a layer from X where the crystals have their long axes parallel with the plate surface, to Y where most of the crystals have their long axes normal to the plate surface.

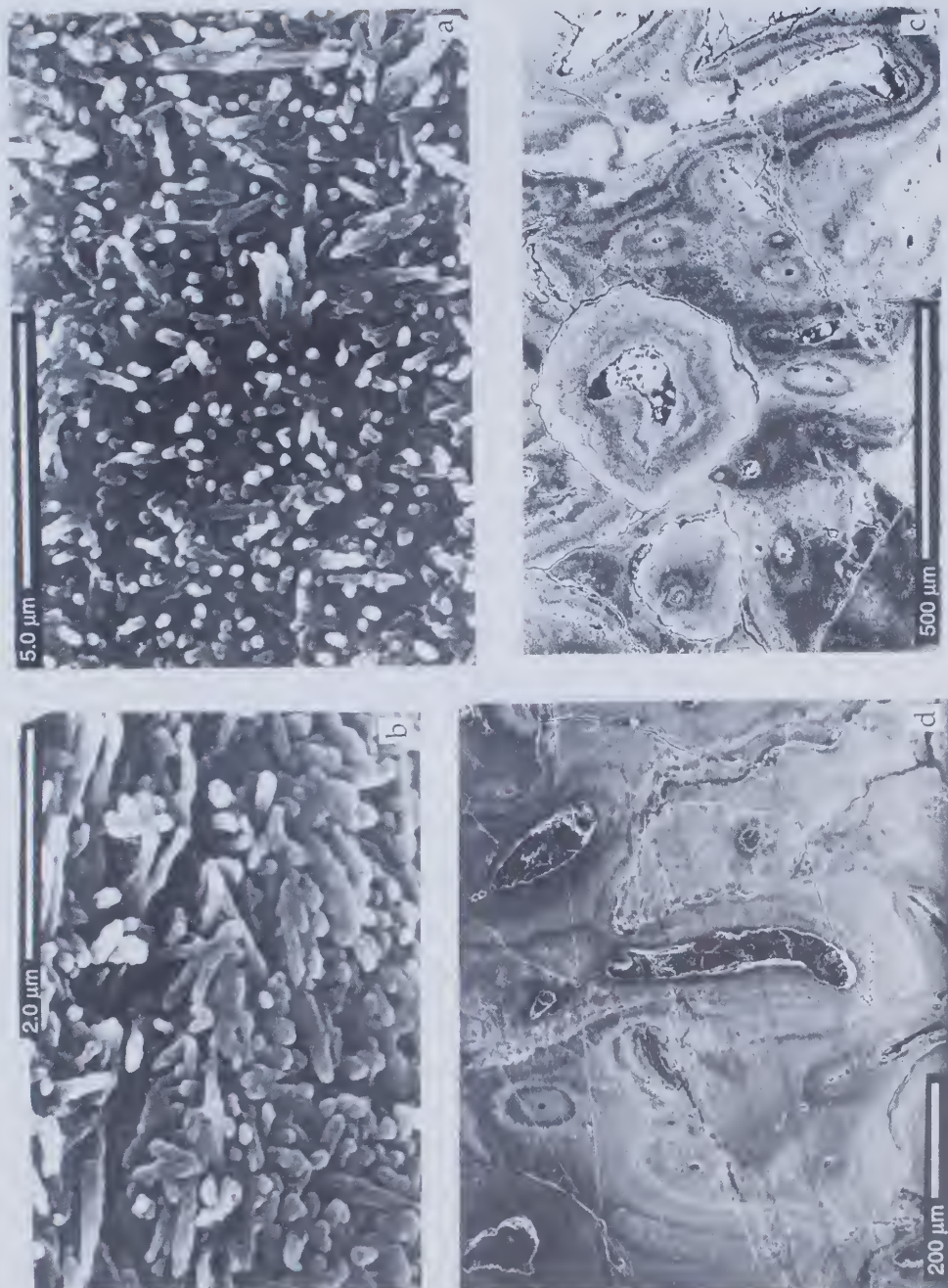


Figure 12 Landscape image with the buccal surface towards the left side of the Figure. (a). back scatter SEM image showing most crystals on the left with axes normal to the page, and more elongate crystals on the right. (b). a greater enlargement showing randomly oriented crystals. (c–d). In (c) the vascular canal in the centre and the one on the left have reversal edges around them transecting the dentine layers in the surrounding material. Note the small dark spots which represent almost completely filled branches of the vascular canals. On the right side of the Figure note the elongate vascular cavity with the concentric layers of tissue surrounding it. Elsewhere on the Figure note the small formerly vascular spaces now almost completely filled with layered tissue. (d). Similar view to (c) with layers of tissue surrounding several vascular canals. Interpretation of both (c and d) given on Figure 13.

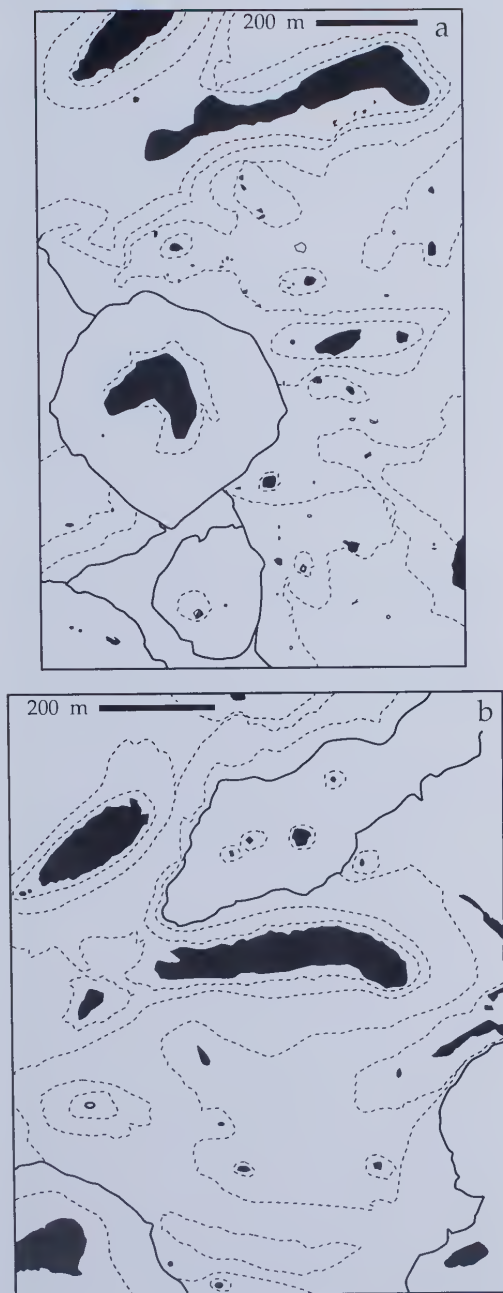


Figure 13 Drawings of Figures 12 c–d showing the layers of dentine, the margins of resorption spaces into which new dentine grew, and the vascular bundles in black. Some small vascular bundles have been filled with dentine. Some of the layered bands are shown by dotted lines, their position indicating the shapes of the layers and their transgression by thick black reversal lines.

the tooth plate during the development of the mandibular dental plates. The same kind of structure is found in *C. australis*, but it is not present in *Dipnorhynchus*. In that genus the whole structure is found to be covered in the internal face of the mandible with small denticles of approximately even size, which we interpret to be an initial variety of such denticles (Campbell and Barwick 2000, Figure 10D).

RELATIONSHIPS

At first sight, this genus is very reminiscent of *Dipnorhynchus sussmilchi* and *D. kurikae*. The external surface, where preserved, is cosmine covered, the median length in the mandible is high, the dental plates are made mainly of bone and thickened dentine on the buccal surface, the posteromedial edge of the prearticulars is formed of a well rounded tuberosity based on bone, the anterior furrow is well developed, the adductor fossa is large and the palate is large and is completely lacking in real teeth. In particular, the structure of the dental plates is very different from any dipnoan apart from the dipnorhynchids. Only the primitive dipnorhynchids have plates in which, at the lateral margins of the plate, the gross form is altered by addition of new material differentially to the contact between the dental plate and the underlying bone. This produces a dental structure that is thick and made of complex material. The lateral margins of the dental plates grow by the addition to the margins of small projections made of the same material as the plates themselves. For this reason alone we consider that *Dipnotuberculus* must be placed in the Dipnorhynchina

On closer inspection, some differences from other members of the Dipnorhynchina are apparent. These are:

1. no dermopalatine plates are fused into the palate;
2. the braincase walls are not fused to the top of the palate;
3. the posterior wall of the skull is not heavily ossified;
4. the median-posterior end of the dental plates on the prearticulars stop well short of the posterior end of the mandible;
5. the lateral marginal ridges on the prearticular plates are absent or poorly developed;
6. the anterior furrow is open posteriorly;
7. the hard tissue of the pterygoids is not so strongly ossified, and where the surface has been eroded away, coarsely tubercular bone is widely exposed;
8. there are no thick ridges in the adductor chamber of the mandible for the attachment of adductor muscles;
9. no large process is present on the dorsal palate;

10. the preorbital/postnasal process was not ossified, but was probably formed of cartilage.

As (Westoll 1949) showed, the evolutionary history of Palaeozoic dipnoans shows many features in common across the whole range of genera. Many of these features were outlined in tabular form by Westoll, and among the skull and mandible characters he listed 17 features that changed. Some of these features associated with the dermal bones of the skull, are not preserved on the Moroccan material, but others are well preserved. Taking into account the discoveries of Westoll and the new information which has been developed in the subsequent 50 years, we note that items 1, 3, 4, 6, 8, 9 and 10, are features that occur in a variety of dipnoans. In this sense such features are of little value in estimating relationships, and if these were fed into a database they would dominate the features we consider to be fundamental to the analysis of the material. The structure of the dental plates alone allows us to signify its position without reference to a cladistic analysis. We have not done such analysis, for the reasons given above, and we regard this new species as being a member of one of the three basic types of dipnoans recognised by Campbell and Barwick (1990).

Dipnotuberculus is regarded as a development of the basic type represented by *Dipnorhynchus*. Should this be so, it is clear that the group of dipnorhynchids split up into the chirodipterid and Moroccan types prior to the late Middle Devonian. This is not surprising, as the method of breaking down food by radial tooth plates is probably much more efficient than the large tubercles observed in dipnorhynchids. In fact, radial tooth rows developed from bony dipnorhynchid plates as shown by *Speonesydrion*, and radial patterns also appear in other groups of organisms which used their palates for biting. Examples are the holocephalans and some sharks. The radially arranged tooth rows with new material added at the ends of each row, provides a basis for rapid change in dental patterns and also for easy modification of wear.

Another point which supports the dipnorhynchid interpretation is the absence of a separate parasphenoid on the buccal surface in this new form. Campbell and Barwick (1985, 2000) have shown that in *Dipnorhynchus*, no separate parasphenoid is present on the buccal surface between the posterior end of the pterygoids, and other specimens of the same genus have confirmed this interpretation. Some specimens of *D. kurikae* show a possible edge on the parasphenoid on the dorsal surface of the palate where the braincase has been removed during preservation, but this shows the edge of the parasphenoid as lying just in front of the buccohypophyseal canal. In another member of the oldest group,

Sorbitorhynchus, a suture has developed between the pterygoids and a clear parasphenoid is present. We note that in *Dipnotuberculus* no sign of any breaks appear on the broken surface across the palate, and in this respect it is more like *Dipnorhynchus*. The dorsal opening for the buccohypophyseal canal is present on a ridge as normally occurs in *Dipnorhynchus* and in *Uranolophus*, but no evidence of such a break occurs in its vicinity. We conclude that the buccal surface of the palate was a single structure without any sign of a median or parasphenoidal sutures. The dorsal surface of *Dipnotuberculus* available to us is too poorly preserved to determine if any parasphenoidal boundary is present as in *D. kurikae*. So far as we are aware, this arrangement of the parasphenoid in ventral and dorsal views, occurs only in dipnorhynchids.

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Culeolus herdmani Sluiter, 1904 (Ascidacea, Tunicata) from the northwestern Australian continental slope with an overview of the genus

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Abstract – Thirteen specimens of *Culeolus herdmani* Sluiter, 1904 (Ascidacea, Tunicata) taken at 3 locations on the northwestern Australian continental slope (between 408m and 550m and 14°16.8'S and 16°09.5'S) are the first records of this genus from Australian waters. The species is one of 7 *Culeolus* spp. recorded at depths of 1800m or less. The newly recorded specimens generally resemble the type specimen and others from the Philippines, Japan and New Caledonia, although there are some differences in the number of branchial folds, length of stalk, presence of a long ventral branchial tentacle and mid-ventral papillary crest and interruption of the postero-lateral papillary crest over the dorsal mid-line. Included in this account is a key to the species of the genus and a table summarising their distribution and characters

INTRODUCTION

The genus *Culeolus* (Pyuridae, Stolidobranchia) was erected by Herdman (1881) for 5 species taken by HMS *Challenger* from depths of 4000 to 5798 m in the Pacific (off Japan, in the tropics and the South Pacific) and the Atlantic Oceans. The genus is characteristic of abyssal ascidians, having an open meshwork of longitudinal and transverse vessels in the branchial sac and lacking stigmata. All species have a narrow stalk that most often is long and wiry and is attached at the anterior end of the body as in other stalked forms (see Kott 1989). The branchial aperture is antero-dorsal and the atrial aperture a large transverse postero-dorsal opening. Most of the species in the genus have a crest of enlarged papillae around the posterior end of the body, sometimes enclosing the atrial aperture but in other species interrupted over the dorsal surface and terminating each side of the atrial aperture. As in other Pyuridae, branchial tentacles are branched, the branchial sac has 5 to 7 folds and the gut forms the usual loop and has liver lobules in the pyloric region. Gonads are relatively long, sometimes with the testis follicles divided into clumps on the mesial surface of the ovarian tube but occasionally the whole gonad divided into hermaphrodite blocks as in *Pyura* and *Microcosmus*. There are seldom more than 3 gonads per side. Occasionally one or more of the gonads on the left side of the body are outside the gut loop. Antero-posteriorly flattened languets are at the junctions of the transverse vessels along the dorsal mid-line.

The species in this genus are relatively uniform in external appearance. Distinctions often are based on the form of papillae both on the surface and in the postero-lateral papillary crest. Useful information

on species relationships can be obtained from the gonads, although in some cases these have not been described; and because relatively few specimens are available in most of the known taxa, variations in the number and arrangement of the gonads and their subdivisions are not well documented.

Unlike most abyssal species, *Culeolus* spp. generally have a relatively restricted known range, with few exceptions being known from either the northern or southern Atlantic or Pacific Oceans, the tropical Pacific or the Southern Ocean. The present species is known mainly from the continental slopes in the western Pacific. The only other species recorded only from slope locations are *C. gigas* Sluiter, 1904, *C. quadrula* Sluiter, 1904, and *C. thysanotus* Sluiter, 1904 from Indonesia; *C. caudatus* Monniot & Monniot, 1991 from off New Caledonia; *C. wyville-thomsoni* Herdman, 1881 from the South Pacific; and *C. sluiteri* Ritter, 1913 from off the Aleutians. All other species of the 21 known in this genus are recorded from 2000m or more (up to 7000m in the Kurile Trench: *C. robustus* Vinogradova, 1970).

TAXONOMY

Culeolus herdmani Sluiter, 1904

Culeolus herdmani Sluiter, 1904: 105. Van Name, 1918: 83. Tokioka, 1953: 289. Millar, 1975: 319. Monniot & Monniot, 1991: 421.

Distribution

New Records

Western Australian (NW of Collier Bay, 14°7.5'S;

122°29.4'E to 14°6.8'S; 122°31.7'E, 408m, WAM 605.88, 1 specimen; W. of Cape Leveque, 16°09.5'S; 120°08.8'E, 550m, WAM 1001.89 4 specimens, 1002.89 2 specimens; WNW Lacepede Archipelago, 15°40.2'S; 120°37.3'E to 15°42.6'S; 120°34.6'E, 500m, WAM 1009.89 6 specimens). The specimens were taken by large trawl on soft bottoms, coll. S. Slack-Smith on F. V. *Soela*, 3.2.84, 18.2.84 and 10.11.84.

Previously Recorded

Indonesia (Sluiter 1904). Philippines (Van Name 1918). New Caledonia (Millar 1975, Monniot & Monniot 1991). Sea of Japan (Tokiooka 1953).

Description

External Appearance (Figures 1–4). Specimens are of similar size, with a translucent head 3 to 4 cm long on a hard wiry stalk to 20cm long. The stalk may gain some of its strength from the mud crowded into a thin rod along one side. The opposite side (continuous with the ventral surface of the head) is gelatinous and slightly concave. The top of the stalk is covered with a thin layer of the translucent body test, where the hard wire-like part is inserted into the test along the anterior end of the head toward the antero-dorsal branchial opening. In life, the antero-posterior axis of the head probably is at right angles to the stalk, with the branchial (incurrent) aperture a transverse opening just above the upper tip of the stalk. In one specimen the upper, broad, flat, crescent-shaped posterior lip of the opening is folded back against the body, but when closed it folds down over the straight, relatively thick and rounded lower lip. The wide transverse arc of the curved atrial aperture, more than halfway along the upper (dorsal) surface, has the concavity of the curve directed anteriorly, probably contributing to the entrainment of the excurrent water by the prevailing currents which flow past as well as through the body from the anterior to the posterior end. The rounded (tongue-shaped) posterior end of the body is slightly wedge-shaped, flattened dorso-ventrally. The postero-lateral crest consists of irregularly placed rounded papillae (2 or 3 across the width of the crest) each about 0.5mm high. The crest extends from each side, near the corners of the atrial aperture, and crosses the mid-line ventral to and just behind the wedge-shaped posterior end of the body. A network of blood vessels beneath the crest has vertical terminal branches extending up into the papillae which are slightly yellowish in the preservative, and may have been a bright colour in life. Slight creases in the surface of the test create a mosaic of blister-like elevations, each low, square, with a minute conical papillum in the centre. A terminal branch of a blood vessel projects into each of these papillae.

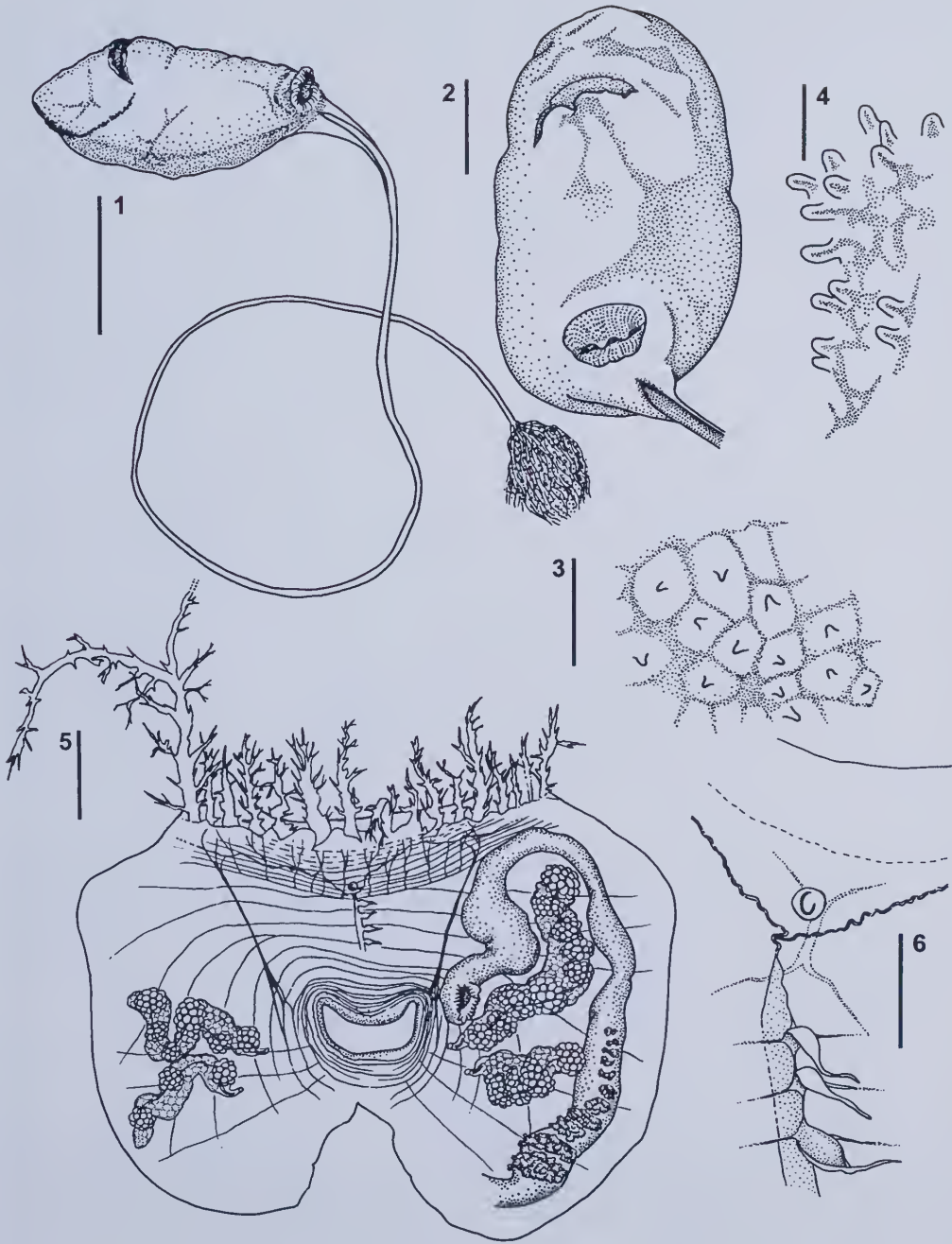
Internal structure (Figures 5,6). The body wall

adheres closely to the test and could not be separated from it. Body musculature consists of short radial muscles from the branchial aperture and very few from the posterior side of the atrial aperture; circular muscles are around each of the apertures; well-spaced parallel transverse muscles cross the dorsal surface between the two apertures and terminate each side of the endostyle; and one conspicuous longitudinal oblique muscle on each side extends from the side of the branchial aperture to the atrial aperture, crossing the transverse muscles and joining the circular ones at each end. Branchial tentacles have long, slender primary branches and short secondary ones. About 12 tentacles of varying length, including a long ventral one, alternate with rudimentary tentacles. The dorsal tubercle is particularly small, circular, at the top of a peritubercular V, with the opening of the neural duct an oblique or reverse c-shaped slit. Six branchial folds are on each side of the body. Two to 9 internal longitudinal vessels are on each fold and one or 2 are between the folds. A branchial formula is DL1(2)1(5)2(9)2(6)1(5)1(3)E. The branchial meshes are longer than wide. Liver lobules are on the edge of transverse lamellae across the pyloric region of the gut. The anal border is divided into small, narrow, crowded lobules. Two long, undivided, undulating tubular ovaries are on each side of the body, in the gut loop on the left and converging to the atrial aperture on the right. Each ovary has up to 9 clumps of testis follicles crowded evenly along the mesial surface. A thickening of the pallial body wall similar to a wide, flat endocarp is on the anterior half of the right body wall antero-dorsal to the gonads.

Remarks

In these specimens the stiff wire-like stalk is inserted into the anterior end of the head, and appears to be placed to support the head at right angles to it, so that the open branchial and atrial apertures are respectively presented to and away from passing currents (see Kott 1989). The force of the currents passing through the large apertures of these organisms would also tend to maintain the position of the body and keep the tentacles, especially the long ventral one, in position in the branchial sac. Also the cross section of the body, flattening out posteriorly, appears to be hydrodynamically adapted for it to be lifted up by passing currents (as an aerofoil wing).

The species resembles the majority in this relatively uniform genus, with similar slender branchial tentacles, 6 branchial folds, open branchial meshes, long ovarian tubes with testis follicles divided into clumps along their surface, the left gonads in the gut loop and a long slender, wire-like stalk. The present specimens generally agree with those of Van Name (1918), Tokiooka



Figures 1–6 *Culeolus herdmani* (WAM 1009.89): 1, Entire animal from right side (stalk folded); 2, body viewed from above; 3, surface test showing rectangular areas with central papillum; 4, papillae of the postero-lateral crest; 5, internal structure showing gut, gonads, musculature and large ventral branchial tentacle; 6, dorsal tubercle and dorsal languets. (scales: 1, 2.0cm; 2, 1.0cm; 3, 2.0mm; 4, 1.0mm; 5, 5.0mm; 6, 3.0mm).

Table 1 Summary of distribution and characters of *Culicoides* spp.

SPECIES	LOCATION	MAXIMUM DEPTH (M)	TEST	PAPILLARY CREST		GONADS			OTHER**
				Postero lateral crest (papillae)	Mid ventral	Number* (R-L)	Condition		
<i>C. robustus</i>	N. Pacific (Kurile Trench)	7000	tough opaque	interrupted dorsally (papillae joined)	papillae joined	2-2	1-3? lobes	short, stout stalk	
<i>C. longipedunculatus</i>	N. Pacific (Kurile Trench)	5000	translucent (continuous ridge)	interrupted dorsally	continuous ridge	1-1	short divided ?	long, fine stalk	
<i>C. tenuis</i>	N. Pacific (Kurile Trench)	6000	small papillae translucent	interrupted dorsally (single row of papillae)	none	3-3	1-5 ? lobes	large open apertures	
<i>C. sluiteri</i>	N. Pacific (Aleutian Is)	600	mounds with a terminal knob	interrupted dorsally (papilla joined)	none	3-1	hermaphrodite blocks		
<i>C. pyramidalis</i>	N. Pacific to California	4867	protruding papillae	interrupted dorsally (single row of papillae)	tuft only	1-1	4-5 ? lobes		
<i>C. murrayi</i>	Japan	5000	crowded tubercles with tufts of processes	encircles atrial aperture (broad-papillated ridge)	broad papillaed ridge	2 or 3-2 or 3 1 or 2 outside	2 or 3 ? lobes	branched stalks <i>C. ushakovi</i> Vinogradova 1941	
<i>C. easteri</i>	Marquesas	5000	small papillae	short band across dorsum	none	2-2 1 outside	1 or 2 ? lobes	stalk inserts along ventrum	
<i>C. gigas</i>	Tropical E. Pacific	924	tough ridge	interrupted dorsally (papillae joined)	papillae joined	1-1	8 ? lobes	short, stout stalk	
<i>C. moseleyi</i>	Tropical Pacific	5000	rough conical or domed papillae	none	none	?	?		
<i>C. herdmani</i>	Japan Philippines Indonesia	200-500 (one record 1700)	quadrate area with central papilla	usually interrupted dorsally (small scattered papillae)	recorded only by Sluiter 1904, Monniot & Monniot 1991	2-2	Up to 8 ? lobe		
<i>C. annulatus</i>	Japan Philippines Indonesia	1994	quadrate area with central papilla	interrupted dorsally (small scattered papillae)	none	?	?	horny skeleton in stalk	
<i>C. quadrula</i>	Japan Philippines Indonesia	694	quadrate area with central papilla	interrupted dorsally (single row of papillae)	none	2-2 1 outside	undivided		

<i>C. elegans</i>	New Caledonia	1480	quadrate area with central papilla	interrupted dorsally (single row of papillae)	none	3 - 2	hermaphrodite blocks	large open apertures
<i>C. thysanotus</i>	Indonesia	450	long vascularised hairs	none	none	1 - 1	5 ? lobes	
<i>C. caudatus</i>	New Caledonia	700	sandy	encircles atrial aperture (vascularised lobes)	none	1 - 1 or 2 1 sometimes outside	12 ? lobes	thick sandy stalk contains extension from body wall in top of stalk
<i>C. recumbens</i>	S. Pacific S. Indian	4000	slight papillae & granular patches	encircles atrial aperture (narrow band papillae)	none	2 to 4 - 2 to 5	short undivided	
<i>C. submi</i>	S. W. Atlantic N. W. Atlantic	5798	minute pointed papillae (velvet-like)	encircles atrial aperture (narrow band of pointed papillae with side scales)	none	1 or 2 - 1 or 2 sometimes outside	to 6 ? lobes	
<i>C. wyville-thomsoni</i>	S. Pacific	1000	irregular elevations with prominent papillae	none	none	?	?	
<i>C. parous</i>	S. W. Africa Scotia Ridge	4893	small spines	none	none	1 - 1	short undivided	
<i>C. pinguis</i>	S. Atlantic	2846	?	encircles atrial aperture	none	2 - 2 1 outside	2 ? lobes	
<i>C. antarcticus</i>	Antarctic	4820	no papillae	interrupted dorsally (papillae joined)	papillae joined		3 - 5 ? lobes	

* in gut loop left unless stated otherwise

** stalk long, narrow and inserts along anterior end of body unless otherwise stated

(1953), Millar (1975) and Monniot & Monniot (1991) assigned to the same species (see also Millar 1975). All these specimens have a similar and relatively restricted geographic range in the western Pacific in relatively shallow water (200 to 500m, once only to 1740m: see Monniot & Monniot 1991); all have similar surface test, body muscles, long and narrow stalk, 2 gonads per side with clumps of testes follicles on the uninterrupted ovarian tubes, and postero-lateral crest of enlarged papillae crossing the ventral surface. Monniot & Monniot (1991) also report the thickened pallial wall and long oblique muscle on each side of the body; and Van Name (1918) reported the long median ventral branchial tentacle (which is fine and inconspicuous and may have been overlooked by other authors). However, there may be some variation in the postero-lateral papillary crest, which usually is interrupted each side of the atrial aperture, but appears to be continuous across the dorsal mid-line anterior to the aperture in specimens from New Caledonia (Millar 1975, Monniot & Monniot 1991). A mid-ventral crest of enlarged papillae (as in the holotype) may have been mistakenly referred to as a mid-dorsal crest in some New Caledonian specimens (see Monniot & Monniot 1991), although other authors have not referred to it. Accounts of the number of branchial folds also vary - Tokioka (1953) reporting 4 on each side and Van Name (1918) and Monniot & Monniot (1991) reporting 4 or 5. Sluiter's holotype has a sandy stalk, shorter than other recorded specimens, and is the only specimen in which spicules have been recorded in the branchial tentacles and branchial sac.

Monniot (1965) had thought that Van Name's (1918) specimens were distinct from *C. herdmani* (as *Culeolus vannamei*) but later (Monniot & Monniot 1991) changed that view.

Culeolus wyville-thomsoni Herdman, 1881 and *C. sluiteri* Ritter, 1913 have irregular or rounded elevations of the surface test, each with a larger central papillum than in the present species (where it is minute and inconspicuous). *Culeolus quadrula* Sluiter, 1904 and *C. elegans* Monniot & Monniot, 1991 from New Caledonia have a similar quadrangular surface pattern, each quadrate area with a minute central conical papillum as in the present species. *Culeolus quadrula* is distinguished by its single row of papillae in the postero-lateral crest and its small gonads with undivided testes. There are no significant differences between the present species (now known from the northwestern Australian, western Pacific continental slopes and Indonesia) and *C. elegans* from New Caledonia, except for the gonads, which in *C. elegans* are divided into hermaphrodite blocks. *Culeolus annulatus* Sluiter, 1904 is also like new Australian material, except that the horny annular rings in the

stalk are not present in *C. herdmani*. The gonads of *C. annulatus* are not known.

Key to species of the genus *Culeolus* Herdman, 1881

1. Crest of enlarged test papillae around the posterior end of the head or across dorsum 2
Crest of enlarged test papillae not around the posterior end of the head or across dorsum 18
2. Crest of enlarged test papillae short, across dorsum only *C. easteri* Tokioka, 1967
Crest of enlarged test papillae crosses ventral midline 3
3. Test tubercles branched with terminal clumps of minute papillae
C. murrayi Herdman, 1881 (Vinogradova 1970, Monniot & Monniot 1982)
Test tubercles not branched and lack terminal clumps of minute papillae 4
4. Stalk thick and body projects into it
..... *C. caudatus* Monniot & Monniot, 1991
Stalk not thick and body does not project into it 5
5. Surface marked off into quadrate areas each with minute central papillum containing terminal ampulla of blood vessel 6
Surface not marked off into quadrate areas each with minute central papillum containing terminal ampulla of blood vessel 9
6. Horny annular rings in stalk
..... *C. annulatus* Sluiter, 1904
Horny annular rings not in stalk 7
7. Gonads divided into hermaphrodite blocks
..... *C. elegans* Monniot & Monniot, 1991
Gonads with ovarian tube undivided 8
8. Testis follicles in clumps
C. herdmani Sluiter, 1904 (Van Name 1918, Tokioka 1953, Millar 1975, Monniot & Monniot, 1991)
Testis follicles not in clumps
..... *C. quadrula* Sluiter, 1904
9. Stalk short, less than twice the length of the body 10
Stalk long, more than twice the length of the body 11
10. Testis clumps about 8/gonad
..... *C. gigas* Sluiter, 1904 (Monniot 1998)
Testis clumps 2 or 3/gonad
..... *C. robustus* Vinogradova, 1970

11. Postero-lateral papillary crest crosses dorsal midline anterior to atrial aperture 12
Postero-lateral papillary crest terminates each side of atrial aperture 14
12. Gonads short with testis undivided
..... *C. recumbens* Herdman, 1881 (Monniot & Monniot 1982, 1991)
Gonads short or long with testis divided into 2 or more clumps 13
13. Gonads on left parallel to endostyle; testis follicles divided into 2 on each ovary
..... *C. pinguis* Monniot & Monniot, 1982
Gonads on left not parallel to endostyle; testis follicles divided into 4 or more on each ovary
..... *C. suhmi* Herdman, 1881 (Van Name 1945; Millar 1955, 1959, 1970; *C. perlatus* Herdman, 1882; *C. tanneri* Verrill, 1885; *C. anonymus* Monniot & Monniot, 1976, 1982).
14. Gonads short, testis follicles not in clumps
..... *C. longipedunculatus* Vinogradova, 1970
Gonads long, testis follicles in clumps 15
15. Enlarged test papillae in mid-ventral line or tuft 16
Enlarged test papillae not in mid-ventral line or tuft 17
16. Mid-ventral clump of enlarged test papillae
.. *C. pyramidalis* Ritter, 1907 (Hartmeyer 1912, Van Name 1945, Millar 1964, Monniot 1998)
Mid-ventral line of enlarged test papillae
C. antarcticus Vinogradova, 1962 (Monniot & Monniot 1982)
17. Papillae on surface of test wart-like, conspicuous
..... *C. sluiteri* Ritter, 1913 (Arnbäck-Christie-Linde 1928, Van Name 1945)
Papillae on surface of test minute, inconspicuous, pointed cones
..... *C. tenuis* Vinogradova, 1970
18. Test covered with long hairs
..... *C. thysanotus* Sluiter, 1904
Test not covered with long hairs 19
19. Surface with crowded conical or dome-shaped papillae or spines 20
Irregular surface with elevated areas each with a prominent central papilla
..... *C. wyville-thomsoni* Herdman, 1881
20. Gonad short, undivided
..... *C. parvus* Millar, 1970
? Gonads long, divided
..... *C. moseleyi* Herdman, 1881 (see Monniot & Monniot 1982 where it is stated that gonads are like those of *C. antarcticus* – the evidence for this is not apparent)

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Leander manningi, a new palaemonine shrimp from Western Australia (Crustacea, Decapoda, Palaemonidae), with a review of the Indo-West Pacific species of the genus *Leander* E. Desmarest, 1849

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Abstract – A new species of marine palaemonine shrimp from Western Australia is described and illustrated. *Leander manningi*, a shrimp closely related to *L. paulensis* (Ortmann, 1897) and *L. tenuicornis* (Say, 1818), was collected during the course of a survey of Cockburn Sound, Western Australia. The Indo-West Pacific species of the genus *Leander* Desmarest, 1849 now known are reviewed and a key for their identification is provided.

INTRODUCTION

The first species of the small palaemonine genus *Leander* to enter the scientific record was *Palaemon tenuicornis* described by Say in 1819 from the North Atlantic Newfoundland Banks. It was re-described as *Leander erraticus* by Desmarest (1849) and first reported from the Indo-West Pacific region, from Japan, by De Haan (1849), as *Palaemon latirostris*. The species was formally placed in the genus *Leander*, as *L. tenuicornis* by Kingsley (1878). Kemp (1925) mentions that, in the Atlantic Ocean, the species occurs as far south as the Falkland Islands. It has since been commonly found throughout the warm waters of the world except for the Eastern Pacific region. The second species to be described was *Leander paulensis* Ortmann, 1897, from Brazil, and half a century later a third, *L. kemp*i was described by Holthuis (1950b) from Indonesian waters. More recently, *L. plumosus* has been described from the Maldives Islands (Bruce, 1994) and since been found to occur in Indonesian, Japanese and New Caledonian seas. A strikingly coloured species, it contrasts markedly with the dull cryptically coloured *L. tenuicornis* and *L. paulensis*. The life colour pattern of *L. kemp*i has not been recorded. A further species from Western Australia is now described and illustrated. Two species are now known to occur in Australian waters.

Abbreviations used: CL, postorbital carapace length; BMNH, The Natural History Museum, London, U.K.; NTM, Northern Territory Museum, Darwin, Australia; RMNH, National Natural History Museum, Leiden, the Netherlands; WAM, Western Australian Museum, Perth, Western Australia; ZMA, Zoology Museum, University of Amsterdam, the Netherlands.

SYSTEMATICS

Leander manningi sp. nov.
Figures 1–4

Material Examined

Australia: Western Australia: 1 female, holotype, BP Oil Refinery Jetty, Kwinana, Cockburn Sound, 0.5m MLW, 11 May 1999, WAM C28204. 2 males paratypes, 1 juvenile male paratype, 1 , WAM C28205, 1 female, *idem*, 7.0m, 1 May 1999, WAM C28206.

Diagnosis

Rostrum moderately deep, far exceeding antennular peduncle, about 1.4 times CL; dentition 2+7/5-6; carapace and abdomen non-setose; third abdominal tergite not posteriorly produced, pleura of fourth segment posteroventrally rounded, fifth acute; stylocerite short, to half length of proximal segment of antennular peduncle; distolateral margin subrectangular, not concave; lamella of scaphocerite well exceeding distolateral tooth; mandibular palp 3-segmented; second pereopod with chela longer than carpus, fingers distinctly shorter than palm, each with small acute proximal denticle, carpus longer than merus; merus and carpus unarmed; third pereopod dactyl stout, about 0.4 of propod length, ventral margin almost straight; propod strongly spinulate.

Description

Small sized palaemonid shrimp, of slender form and with glabrous body.

Rostrum (Figure 1B)

About 1.3 times CL, well exceeding distal

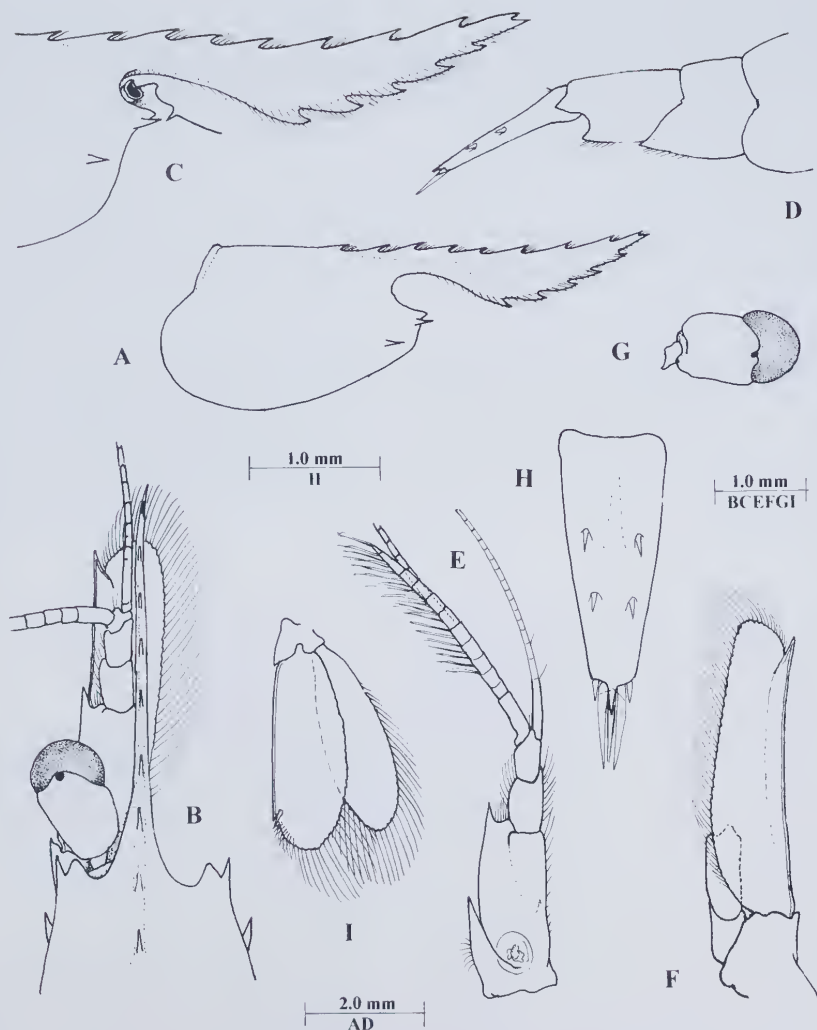


Figure 1 *Leander manningi* sp. nov., female holotype, Cockburn Sound, C28204. A, carapace and rostrum B, anterior carapace and rostrum, dorsal view. C, anterior carapace, rostrum and ophthalmic somite, lateral view. D, fifth and sixth abdominal segments, and telson. E, antennule. F, antenna. G, eye, dorsal. H, telson. I, uropod.

scaphocerite (Figure 1C), with well developed dorsal carina and deep ventral carina, feeble lateral carinae, slightly up-turned distally, dorsal margin with 9 similar acute teeth, first 2 situated on carapace, each with short row of small plumose setae distally, lower margin with 5–6 teeth larger than dorsal teeth, curved, with double row of submarginal plumose setae.

Carapace (Figure 1A)

Smooth, supraorbital spines absent, orbit feebly developed, without post orbital ridge, inferior orbital angle subacute, without inner flange,

antennal spine acute, marginal, exceeding inferior orbital angle, hepatic spine absent, branchiostegal suture absent, branchiostegal spine acute, subequal to antennal spine, postmarginal, below and posterior to antennal spine, tip not reaching anterior carapace margin, anterolateral angle of branchiostegite broadly obtuse, ventral margin non-setose.

Abdomen (Figure 1D)

Third tergite slightly posterodorsally produced, fifth segment about 0.65 of sixth segment length, sixth segment 1.6 times longer

than deep, posterolateral angle acute, posteroventral angle acute, plumose setae ventrally; pleura of first three segments broadly rounded, fourth posteriorly produced, rounded, fifth produced, angular, posteroventrally acute, ventrally setose.

Telson (Figure 1H)

About 0.9 of CL, 1.4 times sixth andominal segment length, 2.5 times longer than anterior width, lateral margins sublinear, posteriorly convergent, dorsally with 2 pairs of small subequal dorsolateral spines, about 0.1 of telson length, at 0.4 and 0.65 of telson length, posterior margin (Figure 4G) about 0.4 of anterior margin width, with long slender apical point, about 0.7 of posterior telson width, 0.1 of telson length, far exceeding tips of lateral spines, with pair of anterodorsal setae, lateral spines similar to dorsal spines, medial spines well developed, subventral, about 0.33 of telson length, with pair of long slender plumose subventral submedian setae.

Antennule (Figure 1E)

Peduncle reaching to about 0.75 of the rostral length; proximal segment about 2.3 times longer than wide, medial margin with plumose setae, with strong acute ventromedial tooth at 0.5 of length, lateral margin feebly convex, with stout distolateral tooth reaching to about midlength of intermediate peduncular segment, anterolateral margin (Figure 4A) moderately produced, bluntly angular, with numerous plumose setae which extend along the subventral lateral border, stylocerite slender, acute, reaching to about 0.55 of segment length, statocyst with granular statolith; intermediate segment about 0.33 of proximal segment length, 1.6 times longer than wide, medial margin laminar, margins with plumose setae, distal segment subequal to intermediate segment length, 2.0 times longer than wide, upper flagellum biramous with proximal 5–6 segments of rami fused, short ramus with 7–8 segments, with about 21 groups of aesthetascs on 10 distal segments, lower ramus slender, filiform, about 36 segments, lower flagellum slender, filiform, about 33 segments, 0.8 of longer free ramus of upper flagellum.

Antenna (Figure 1F)

Basicerite with small acute lateral tooth; ischiocerite and merocerite normal, carpcerite reaching to about 0.33 of scaphocerite length, subcylindrical, 3 times longer than wide; scaphocerite about 4 times longer than proximal width, lamella broad, tapering feebly distally, bluntly angular distally, lateral margin slightly concave, with strong tooth (Figure 4B) distally, not exceeding distal margin of lamella.

Eye (Figure 1G)

Cornea globular, about 0.25 of CL, black, with well developed accessory pigment spot, stalk subequal to corneal diameter, 1.2 times longer than central width. Ophthalmic somite with small blunt angular median process.

Mandible (Figure 2A)

Corpus large, stout, with long slender 3-segmented palp distolaterally (Figure 4C) proximal two segments short, subequal, together subequal to length of subcylindrical setose terminal segment; molar process short, stout, subcylindrical, distally truncate, with 4 large blunt marginal teeth, scaphoid medially; incisor process normal, 3 teeth distally on right, 4 on left, central teeth smaller than outer teeth.

Maxillula (Figure 2B)

Palp (Figure 4D) bilobed, upper lobe with short slender simple seta, lower lobe with small ventral tubercle with minute terminal uncinat setule; upper lacinia broad, distally obliquely truncate with numerous short simple spines and setae distally; lower lacinia short, subcylindrical, tapering, distally truncate, with numerous feebly spiniform setae distally and ventrally.

Maxilla (Figure 2C)

Basal endite well developed, bilobed, lobes short, subequal, with numerous short simple setae distally; coxal endite obsolete, medial margin sublinear; palp short, non-setose; scaphognathite small, 3 times longer than central width.

First maxilliped (Figure 2D)

Basal endite large, broad, distally rounded, with numerous long simple marginal setae distomedially; coxal endite distinct, simple, medially convex with 4 very long setulose setae distomedially; palp short, simple, with single short plumose seta distally; exopod well developed, with large caridean lobe, ramus slender, with numerous plumose setae distally, epipod large, feebly bilobed, distal lobe much larger than proximal.

Second maxilliped (Figure 2E)

Of normal form, dactylar segment 3.5 times longer than broad, with numerous robust serrulate spines medially, propodal segment broad, distally rounded, feebly medially produced, with simple setae and spines distomedially; carpus acutely produced medially; ischiomerus and basis normal; exopod well developed, flagellum slender with numerous plumose setae distally, coxa broadly rounded medially, without ventral process, with several long simple setae medially, with small



Figure 2 *Leander manningi* sp. nov., female holotype, Cockburn Sound, C28204. A, mandible (left). B, maxillula (right). C, maxilla. D, first maxilliped. E, second maxilliped. F, third maxilliped.

rounded epipod laterally with larger multi-lamellar podobranch.

Third maxilliped (Figure 2F)

Extending distally to exceed carpocerite by about half terminal segment length; endopod with ischiomerus completely fused with basis, combined segment about 4.5 times longer than distal width, bowed ventrally, expanded, twisted and flattened distally, distolateral angle with single small spine, medial margin with numerous long simple

spiniform setae, similar setae present laterally; penultimate segment about 0.75 of antepenultimate segment length, subcylindrical, 4.5 times longer than wide, medial margin with numerous long simple spiniform setae, fewer on lateral margin; terminal segment 0.6 of antepenultimate segment length, 5.0 times longer than basal width, tapering distally, with short stout simple spine distally, with 8 transverse rows of serrulate spines ventromedially, longer simple spiniform setae distally and medially; exopod as in second

maxilliped; coxa not medially produced, sparsely spinulate, with oval lateral plate; single small well developed multi-lamellar arthrobranch laterally.

Epistome

Anteriorly vertically angulate, without ventral beak.

Thoracic sternites

Fourth thoracic sternite with small short acute median process. Other sternites unarmed.

First pereopods (Figure 3A)

Normal, extending about level of distal antennular peduncle; chela (Figure 3B) with palm oval in section, slightly compressed, about 1.9 times longer than deep, with 5 rows of serrulate setae proximoventrally, fingers slender, simple, tapering to small hooked tips, lateral entire laminar cutting edge distinct over distal half, obsolete proximally, with sparse groups of simple and serrulate setae; carpus about 1.4 times chela length, 5.5 times longer than distal width, tapering proximally, unarmed, with 4–5 serrulate spines distoventrally; merus about 0.85 of carpus length, 5.5 times longer than central width, greatest width at half length, unarmed; ischium 0.55 of carpus length, 3.2 times longer than distal width, compressed distally, obliquely tapered proximally, with numerous long simple setae along ventral margin; basis about 0.3 of chela length, ventrally biconvex with long simple setae; coxa normal, with small setose distoventral process.

Second pereopod (Figure 3C)

Subequal, similar, exceeding carpocerite by three fourths of carpus, scaphocerite by about length of fingers (in small female specimen), chela (Figure 3D) about 1.05 of CL, palm smooth, subcylindrical, slightly swollen centrally, 3.0 times longer than deep, fingers (Figure 3E) 0.88 of palm length, similar, with small simple hooked tips, cutting edges sharp, entire over distal three-fourths, sparsely setose, dactylus 6.4 times longer than proximal depth, with single small recurved acute tooth at 0.25 of length (Figure 4E), fixed finger similar, smaller tooth at 0.2 of length; carpus 0.87 of chela length, 1.5 times palm length, 5.9 times longer than distal width, tapering proximally, slightly expanded distally, unarmed; merus 0.68 of chela length, 6.2 times longer than central width, subuniform, unarmed; ischium 0.6 of chela length 6.0 times longer than distal width, unarmed; basis and coxa normal.

Third to fifth pereopods (Figure 3F)

Third pereopod of normal form, neither robust nor slender, exceeding carpocerite by distal half of propod, reaching to about distal margin of

intermediate segment of antennular peduncle, dactyl simple (Figure 4F) about 0.42 of propod length, 5.2 times longer than basal width, strongly compressed, acute, unguis feebly defined, dorsal margin convex, ventral margin feebly concave, laminar, entire, with 3 spiniform setae at about 0.75 dorsal margin length, sensory setae present distally medially and laterally; propod (Figure 3G) 9.0 times longer than wide, uniform, with pair of distoventral spines, subequal to propod width (one missing in Figure 4F), 5 spiniform setae distodorsally, 4 single spines of decreasing size proximally along ventral border; carpus about 0.5 of propod length, 4.2 times longer than distal width, unarmed; merus 1.1 times propod length, 8.5 times longer than width, unarmed; ischium subequal to carpus length, 0.55 of propod length, unarmed; basis and coxa normal. Fourth and fifth pereopods similar, fifth propod with normal distoventral spines and numerous serrulate ventral spines.

Pleopods

Male first pleopod (Figure 3H) with basipodite 2.6 times longer than wide, distolateral angle acute, exopod subequal to basipodite length, 4.5 times longer than width, endopod (Figure 4I) 0.65 of exopod length, uniform, four times longer than wide, lateral margin feebly convex, with short plumose setae distally, distal margin similar, rounded, medial margin feebly concave, proximal third with four long plumose setae, middle third with four short curved spinules, distal third with short plumose setae, without appendix interna. Second pleopod (Figure 3I) with basipodite 1.1 times first pleopod basipodite length, 2.6 times longer than width, distolateral angle acute; exopod 1.1 times basipodite length, 4.2 times longer than width; endopod 0.9 of exopod length, 5.0 times longer than width, with appendices (Figure 4J) arising at 0.33 of medial margin length, appendix masculina slender, subcylindrical, slightly swollen distally, about 10 times longer than distal width, with numerous long slender simple spines along ventral surface and distolateral margin to tip, longest spines terminal, about 0.45 of appendix length, reaching almost to endopod end; appendix interna normal, reaching to about 0.6 of appendix masculina length, with few cincinnuli medially. Female first pleopod with endopod about 0.33 of exopod length, without spinules on central third of medial margin.

Uropod (Figure 1I)

Protopodite normal, posterolateral angle acute; exopod distinctly exceeding posterior end of telson, to about tip of submedian spines, with lateral margin straight, with small acute tooth distally (Figure 4H), longer, more slender spine medially, 3.0 times longer than width, broadly rounded

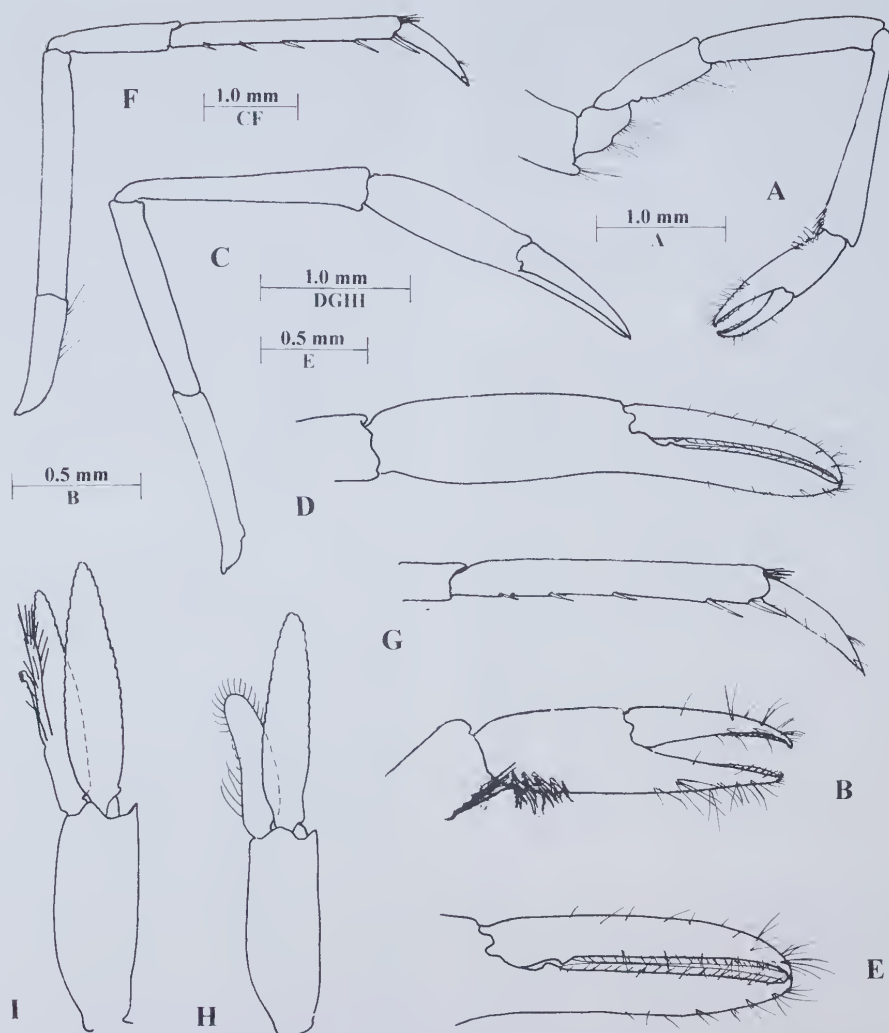


Figure 3 *Leander manningi* sp. nov., female holotype, Cockburn Sound, C28204. A, first pereiopod. B, same, chela. C, second pereiopod. D, same, chela. E, same, fingers. F, third pereiopod. G, same, propod and dactyl. Male paratype, C28205. H, first pleopod. I, second pleopod.

distally, with submarginal row of short setae dorso-distolaterally; endopod about 0.9 of exopod length, 3.2 times longer than wide.

Measurements (mm's)

Holotype: carapace length 3.15mm, carapace and rostrum 7.5mm, total body length (approx.) 18mm, second pereiopod chela 3.25mm. Largest paratype male, CL 4.7 mm.

Colour pattern
Unknown.

Habitat

The specimens were collected from scrapings of marine harbour piles.

Bathymetric range

0.5–7.0 m.

Etymology

The species is named in honour of the late Dr Raymond B. Manning, who, in 1961, re-described *Leander paulensis* (Ortmann).

Distribution

Type locality: Kwinana, Cockburn Sound, Western Australia.

Systematic Position

Closely related to *Leander paulensis* (Ortmann) and *L. tenuirostris* (Say). May be distinguished by: –

1. Smaller number of dorsal rostral teeth, usually 9 (10–14 in *L. paulensis*, 8–14 in *L. tenuicornis*).
2. Anterior border of proximal segment of antennal peduncle feebly produced, far exceeded by distolateral tooth (distinctly produced in *L. paulensis*, not produced, confluent with elongate lateral tooth in *L. tenuicornis*).
3. Scaphocerite distally broad, with lamella exceeding distolateral tooth. (distally attenuated, with distolateral tooth distinctly exceeding lamella in *L. paulensis*).
4. First pereopod with fingers subequal to palm (much longer than palm in *L. tenuicornis*, similar in *L. paulensis*).
5. Second pereopod with palm not swollen (palm swollen in *L. tenuicornis*), with fingers shorter than palm length (longer in *L. tenuicornis*, similar in *L. paulensis*), cutting edge of dactyl with single small acute tooth proximally (2 small rounded teeth in *L. paulensis*, single small tooth in males in *L. tenuicornis*); carpus distinctly longer than palm and merus (of similar length to palm and shorter than merus in *L. paulensis*).
6. Comparatively short stout dactylus on ambulatory pereopods, about 5 times longer than basal width, with sharp laminar ventral margin (about 10 times longer than basal width in *L. paulensis*, with obsolete ventral lamina).

Remarks

The specimens are unfortunately not in a good state and of the five specimens only two have a fully developed second pereopod preserved (one specimen has both second pereopods in an early stage of regeneration). The largest female (WAM C28206 CL 4.8 mm) lacks most of the rostrum and has only one attached first pereopod and both detached fifth pereopods. The specimen (WAM C28204 CL 3.15) with a single second pereopod and an intact rostrum is selected as the holotype. The smallest specimen (WAM C28205 CL 2.4) has both second pereopods, with the chelae about 0.33 of the CL: the second pleopod has a rudimentary spineless appendix masculina. Only a single arthrobranch was observed on the third maxilliped in the dissected specimen, but a second may have been lost or destroyed during dissection.

Leander manningi differs from the diagnosis of the genus given in Chace and Bruce (1993). This states that in this genus the fourth thoracic sternite is unarmed and that an appendix interna is present on

the male first pleopod. In *L. manningi* a small median process is present on the fourth thoracic sternite and the endopod of the male first pleopod lacks an appendix interna. However, a medial sternal process is present on the fourth thoracic sternite in *L. plumosus*, although this species does have an appendix interna on the male first pleopodal endopod (Bruce, 1994). Holthuis (1950a) confirms the presence of an appendix interna on the male first pleopod in *L. tenuicornis* and Ramos-Porto (1986) in *L. paulensis*. The situation in *L. kemp*i was not reported by Holthuis (1950b) as all specimens were female. These discrepancies are not sufficient to prevent the inclusion of *L. manningi* in the genus *Leander*. Although not previously reported it may be noted that no sternal process can be discerned on the fourth thoracic sternite in *L. paulensis* and that the distoventral processes of the first pereopod coxae are noticeably well developed. The *Siboga* paratypes of *L. kemp*i have been re-examined in this study. Holthuis (1950b) reported that the carapace "is smooth, though short and rather stiff hairs often are scattered over its surface" and the "abdomen smooth, similar hairs as on the carapace present here, they are even more numerous especially on the posterior segments", and "The pubescence of the body of *L. kemp*i, especially the abdomen, is not observed in *L. tenuirostris*". No trace of these setae can now be detected in these specimens and the body is completely glabrous, as in the other species of the genus other than *L. plumosus*. The larger ovigerous specimen has a CL of 9.1 mm, and the fourth thoracic sternite bears a small short conical median process. The ventral rostral border also bears a double row of submarginal plumose setae, as in the other species of the genus, and not a single row.

The mouthparts of *L. manningi* in general closely resemble those of the type species of the genus, *L. tenuicornis*, as illustrated by Holthuis (1950a, 1950b). The main differences are: the palp is 3 segmented; the maxillula has the palp with a smaller setose upper lobe and a more blunt lower lobe with a small setiferous tubercle distoventrally, the lower lacinia is distinctly more slender; the maxilla has the basal endites subequal and similar, broader; first maxilliped with basal endite less elongate, coxal endite with 4 long plumose setae distomedially; second maxilliped with propodal segment shorter and broader, epipod smaller, podobranch less developed.

A revised diagnosis for the genus *Leander* is: palaemonine shrimps with rostrum well developed, lacking elevated basal crest; hepatic spine and branchiostegal suture absent, postmarginal branchiostegal spine present; mandible with palp; second pereopods normally subequal, similar; ambulatory dactyls simple, shorter than propods. The species closely resemble *Palaemon* species, but these may generally be distinguished by the

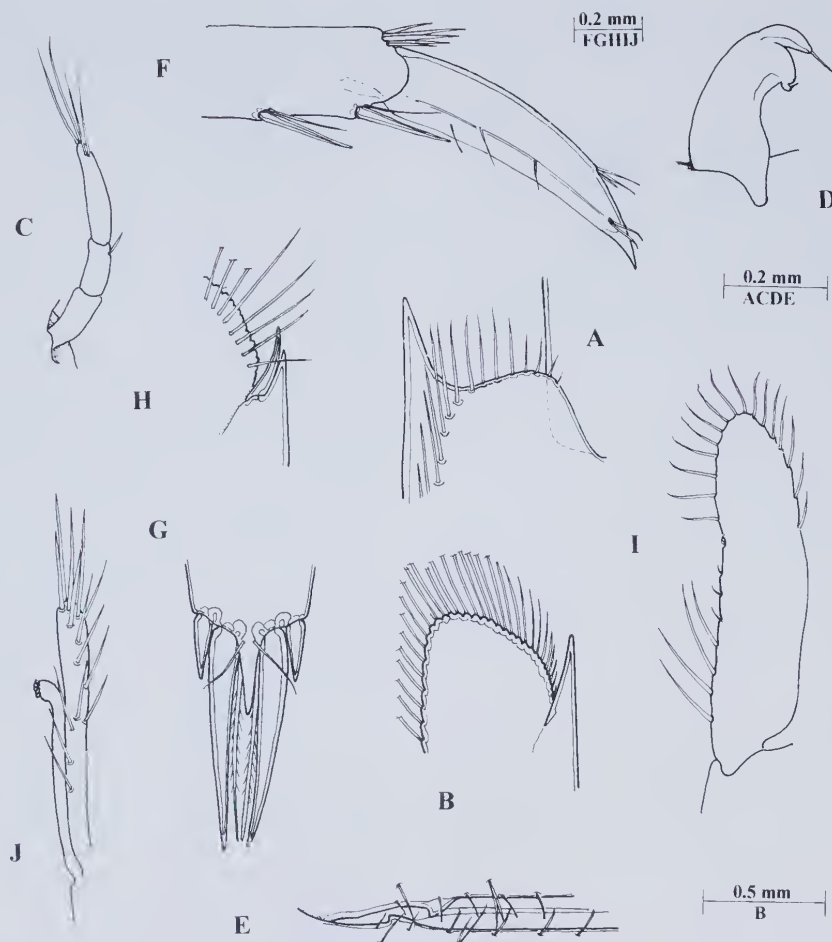


Figure 4 *Leander manningi* sp. nov., female holotype, Cockburn Sound, C28204. A, proximal antennal segment, distolateral margin. B, scaphocerite, distal margin. C, mandibular palp. D, maxillula, palp. E, second pereiopod, proximal cutting edges of fingers. F, third pereiopod, dactyl and distal propod. G, posterior telson margin. H, uropod, distolateral exopod. Male paratype, C28205. I, first pleopod, endopod. J, second pleopod, endopod, appendix masculina and appendix interna.

presence of a distinct branchiostegal suture and generally a marginal branchiostegal spine. In the type species of the genus *P. adpersus* Rathke it is submarginal.

The figures of *L. tenuicornis* provided by Ledoyer (1984) suggest that the fourth pleuron is more angular than in *L. manningi* or *L. paulensis*, and that the ventral border of the ambulatory propod is armed with a double row of ventral spines, not present in these species.

Leander Demarest, 1849

Leander E. Desmarest, 1849: 92. Type species:

Leander erraticus Desmarest, 1849, junior synonym of *Palaemon tenuicornis* Say, 1818, by original designation and monotypy. Gender masculine.

Key for the identification of *Leander* species.

1. Rostrum greatly exceeding carapace length ($\times 2.5$ in males, $\times 1.75$ in females); carpus of second pereiopod distinctly longer than chela; R. 2+9-10/9-12 *Leander plumosus* Bruce
- Rostrum not exceeding 1.5 times carapace length; carpus of second pereiopod shorter than or not greatly exceeding chela length..2

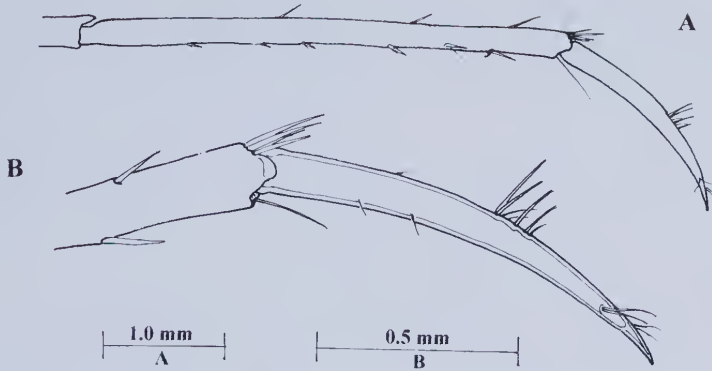


Figure 5 *Leander paulensis* (Ortmann), A, third pereiopod, propod and dactyl. B, same, distal propod and dactyl.

2. Ambulatory dactylus elongate, slender, *ca* 10 times longer than basal width; R. 3+8-11/5-7 *Leander paulensis* (Ortmann)
– Ambulatory dactyls robust, short, *ca* 5 times longer than basal width 3
3. Fifth pleuron posteroventrally rounded; R. 2+10-12/5-7 *Leander kemp*i Holthuis
– Fifth pleuron posteroventrally acute 4
4. Anterolateral tooth of proximal segment of antennal peduncle reaching to level of half length margin of second segment, stylocerite not far exceeding half proximal segment length R. 2+7/5-6 .. *Leander manningi* sp. nov.
Anterolateral tooth of proximal segment of antennal peduncle reaching to level of distal margin of second segment, stylocerite far exceeding half proximal segment length; R. 8-14/5-7 (rostrum sexually dimorphic)
..... *Leander tenuicornis* (Say)

The following species are known from the Indo-West Pacific region:

***Leander kemp*i Holthuis, 1950**

*Leander kemp*i Holthuis, 1950b: 31–34, figure 3. — Chace and Bruce, 1993: 6.

Types

1 ovig. female holotype, RMNH D 6858; 2 (1 ovig. female) paratypes ZMA, De. 102802.

Type localities

Siboga station 121, Manado, Sulawesi, and *Snellius* station, Beo, Kepulauan Talaud, Indonesia.

Bathymetric range

To 55m (Holthuis, 1950b).

Distribution

Indonesia: Known from the original description only, from Manado, Sulawesi, and Beo, Kepulauan Talaud.

Remarks

In the original description of this species, Holthuis (1950b) did not designate type material. This was done by Franssen, Holthuis and Adema (1997), in which the Talaud Islands specimen was chosen as the holotype.

***Leander manningi* sp. nov.**

See above.

***Leander plumosus* Bruce, 1994**

Restricted synonymy

Leander plumosus Bruce, 1990, 62–62; 1994: 39–48, figures 1–5, 6AB, plate 2.

Types

Holotype female, NTM Cr.8567A; paratype, dissected male, NTM Cr.008567B.

Type locality

Ari Atoll, Maldives Islands.

Bathymetric range

From 3m (Minemizu, 2000); 7m (Bruce, 1994, 1996; Okuno and Ono, 1998); 15m (Gosliner *et al.*, 1996).

Distribution

Maldives Islands (Bruce, 1994). **Indonesia:** Bali, (Bruce, 1990; Steene, 1990; Debelius, 1999); Flores (Debelius, 1999). **Japan:** Ryukyu Islands, Ishigaki Island, Yaeyama group, and Kerama Islands

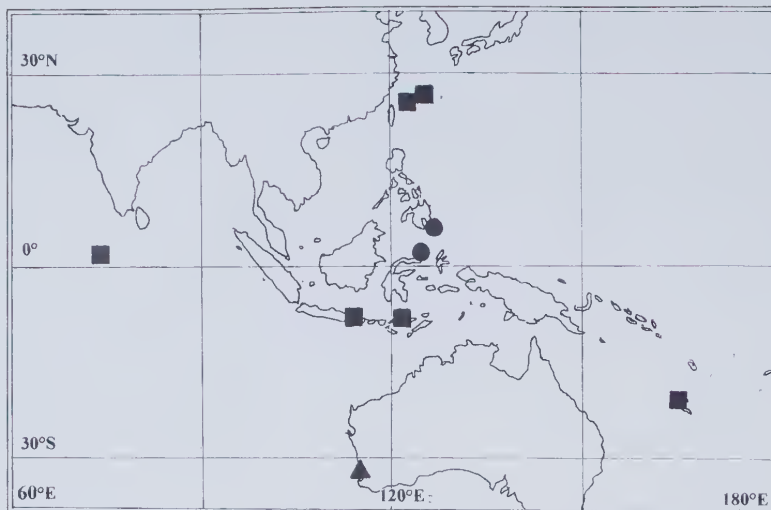


Figure 6 Distributions of *Leander kemp* (●), *Leander plumosus* (■) and *Leander manningi* (▲).

(Okuno and Ono, 1998). New Caledonia: Senez Reef (Bruce, 1996).

Leander tenuicornis (Say, 1818)

Restricted synonymy

Palaemon tenuicornis Say, 1818: 249.

Leander erraticus Desmarest, 1849: 92.

Leander tenuicornis — Kingsley, 1978: 122. — Kemp, 1925: 302–304, figure 11. — Holthius, 1950a: 26–28, figures 1–2; 1950b: 155–167, pls 41, 42. — Ledoyer, 1984: 25, figure 9. — Ramos-Porto, 1986: 13–16, figures 5–6. — Chace and Bruce, 1993: 6–7. — Holthuis, 1993: 108 figure 95.

Types

"The type specimens are preserved in the collection of the Academy of Natural Sciences at Philadelphia" (Holthuis, 1950), and are now reported as lost (Boyko, personal communication, 17 January 2001). Two syntypes, also can not now be located in the BMNH collections (M. Lowe, personal communication, 27 January 2001).

Type Locality

Newfoundland Banks.

Bathymetric range

Shallow water, in sea grass beds and algae, frequently in floating *Sargassum*.

Distribution

Widespread throughout most tropical, subtropical

and some temperate waters. From Atlantic: Newfoundland to Brazil; Mediterranean Sea. Indo-West Pacific: Red Sea to South Africa, east to Japan, Philippines, Caroline Islands, and New Zealand (Chace and Bruce, 1993). Numerous records from Australian waters. Not recorded from the Central Pacific east of Palau or the East Pacific region.

Remarks

The Falkland Islands record (Kemp, 1925) has never been verified. Kemp does not indicate the origin or present whereabouts of the specimens upon which this report is based. Holthuis (1952: 73), states "Miers (1876: 86) remarks that *Palaemon affinis*, which species is named *Leander affinis* by him, occurs on the Falklands. This is, however, very improbable since the species at present is known from New Zealand only. Miers's specimen may have been incorrectly labelled or misidentified. *Leander tenuicornis* (Say) for the first time has been reported from the Falkland Islands by Kemp (1925: 304). Since that time the species has no more been recorded from that region."

ACKNOWLEDGEMENTS

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Melitid amphipods of Barrow Island, Western Australia Part II – recent discoveries

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Abstract – Investigation of new sites of underground waters on Barrow Island, Western Australia, yielded amphipods of the families Melitidae and Bogidiellidae at seven locations not previously sampled. Described species of the genus *Nedsia*, family Melitidae, were found at several of these locations; three new species of the genus are described from two sites. Keys to the known species of *Nedsia* are extended to include the three new ones.

INTRODUCTION

Barrow Island, Western Australia, 20°46'S, 115°24'E, is an isolated extension of the Cape Range, situated approximately 55 km west of the mainland coast. Little, or no surface water is to be found across the greater area of the island, and permanent surface waters are absent. Aquatic invertebrates nevertheless abound, but are restricted to cave systems and ground water, which are widespread. As reported previously (Bradbury and Williams 1996a, b, 1997; Humphreys 1993a,b, 1999, 2000), extensive sampling, commonly associated with oil exploration and exploitation, has revealed the frequent presence of amphipod species. In all, seven species of the genus *Nedsia* (Barnard and Williams 1995) attributed to the family Melitidae, one species of the genus *Bogidomma* (Bradbury and Williams 1996a), family Bogidiellidae, and one species of the genus *Liagoceradocus*, family Hadziidae, have been described from Barrow Island (Bradbury and Williams 1996b).

Amphipod species of the melitoid (hadzioid) complex are distributed widely over the continent (Bradbury and Williams, 1999). The melitoid (hadzioid) complex is not, however, clearly demarcated and has been the subject of review for some time, as yet without resolution. For the time being, therefore, and following Barnard and Williams (1995), taxa described here are attributed to the family Melitidae. Melitids of Barrow Island, the Nullarbor Plain and the Flinders Ranges all appear to be marine strandings and/or invaders from periods of inundation during the Cretaceous, between 120 and 100 million years ago (Bradbury and Williams, 1997; Paine, 1990). These once marine regimens encompass much of inland Australia, as well as many coastal regions, and considerable numbers of new species might reasonably be expected among collections yet to be analysed;

eleven species have been described to date (Barnard and Williams, 1995; Bradbury and Williams, 1996a; Bradbury and Eberhard, 2000). All such melitids are hypogean and have well developed stygobiont characteristics, including blindness, lack of pigmentation, fragility and attenuation of the appendages (Holsinger, 1994), and in some regions display considerable endemism (Bradbury, 2000).

This paper reports on the analysis of a further twenty samples, taken between October 1998 and April 1999, from seven sites on Barrow Island. Three new species of the genus *Nedsia*, family Melitidae are described. All are small, ranging in size between 2 and 4 mm. Species of the family Bogidiellidae were also present in small numbers; these shall be described at a later date.

METHODS OF DISSECTION AND DESCRIPTION

The notation M, with an appended number, indicates the position of an object as a fraction of the distance from the base to the apex of an appendage; S large spine; s, small spine. Abbreviations used in the figures are as follows: A, antenna; Abd, abdomen; acc, accessory; C, coxa; d, dorsal; dact, dactylus; E, epimeron; fl, flake; flag, flagellum; g, gill; G, gnathopod; Hd, head; i-, inner; juv, juvenile; L, left; lac, lacinia mobilis; LL, lower lip; MD, mandible; med, medial; mol, molar; MP, maxilliped; MX, maxilla; o, outer; O, oostegite; opp, opposite; p, palp; P, pereopod; PC, prebuccal complex; pl, plate; Pp, pleopod; R, right; sp, spine; sq, square view; sr, setae removed (sometimes marked by sockets); st, sternal gill; T, telson; U, uropod; UL, upper lip; UR, urosome; 1, 2, 3 ..7, first, second, third ..seventh article, segment, somite or epimeron (as appropriate) (Bradbury and Williams,

1997). Mandibular palp setae are described using the notation of Karaman (1969) and Barnard and Barnard (1983). WAM: Western Australian Museum. BES: Field numbers of the biospeleology collection at WAM.

Results

Collection sites, positions and collectors are shown in Appendix 1. The majority of locations yielded few – in many cases single – specimens, many of which were immature or damaged, making unequivocal identification impossible. Three new species were detected, each from sites yielding relatively high numbers, and in each case, sympatric; *Nedsia chevronia* sp. nov. with *N. hurlberti* Bradbury and Williams, and the other case sympatry between *Nedsia halletti* sp. nov. and *Nedsia stefania* sp. nov.

Although specimens were in many cases damaged or immature, the following described species were identified among the collection: *Nedsia hurlberti*, collections 3395, 3397; *N. humphreysi*, collection 6969; *N. straskraba*, collections 3407, 3420, 3439; *N. sculptilis* / *N. macrosculptilis*, 6980, 6983, 6984, 6990, 7001. Sample 7308, a single small specimen, is probably of a new species. New species are described from samples 3424, 3441, 3462.

SYSTEMATICS

Family Melitidae Bousfield, 1973

Nedsia chevronia sp. nov.

Figures 1–3

Type locality

Underground water, MW15, Barrow Island, Western Australia, 20°46'58"S, 115°27'53"E.

Material examined

Holotype

♂, 'a', 4 mm (WAMC 28207) Western Australian Museum field collection number BES 3424, 20°46'58"S, 115°27'53"E, 23 October 1998, W. F. Humphreys and S. M. Eberhard.

Paratypes

♂ 'b', 3.5 mm (WAMC 28208) 3 other ♂♂ 2.5–3.0 mm (WAMC 28311). Same data as holotype.

Other material

17 specimens, all small, all damaged (WAMC 28312), Barrow Island, Western Australia, Western Australian Museum field collection number BES 3395, 20°46'58"S, 115°27'53"E, 22 October 1998, W.F. Humphreys and S.M. Eberhard.

Diagnosis

Pleonites with few dorsal setae. *Head*: rostrum obsolescent; lateral cephalic lobes moderately projecting, very broad; no antennal sinus present; eyes absent. *First antenna*: longer than A2; ratio of peduncular articles from 7:6:3; accessory flagellum 2 articulate. *Second antenna*: short; flagellum much shorter than peduncle; calceoli absent. *Mandible*: palp reduced, 2 articulate; ratio of mandibular palp articles 1:1, article 1 not setose, terminal article tapered, sub-truncate; setae 2 E. *Upper lip*: symmetrical. *Lower lip*: with inner lobes. *Mandibles*: 4 accessory blades (rakers), with inter-raker plumose setae between each main raker. *Maxillae*: moderately setose medially; inner plate of maxilla 1 ovate with 5 medial setae, outer plate with denticulate setae, palps symmetric, with thin apical setae; inner plate of maxilla 2 with row of medial setae extending onto face apically, other medial setae few. *Maxilliped*: outer plate with no blunt naked tooth setae continuous with distal plumose setae, palp article 3 apex not produced, dactyl with moderate length nail. *Coxae*: short, broader than long, with few posterior setae. *Gnathopods* diverse. *First Gnathopod*: palm transverse; setae at corner of palm = lateral 2 long, medial 4 short. *Second Gnathopod*: propodus palm defining corner with 2 setae laterally. *Pleopods*: similar; rami extending equally, basomedial setae of inner rami bifid; retinaculæ 2, no accessory retinaculum present. *Epimera*: postero-ventral tooth of epimera 1–3 absent; posterior margins smooth; E2–3 bearing facial setae near ventral margin. *Uropods*: apico-lateral corner of peduncles on uropods 1–2 with 2 setae; dorsal margins with setae; rami of uropods with no or one setal rows; outer ramus of uropod 3 with distal peduncular setae; inner ramus reaching to M0.17 on article 1 of outer ramus. *Telson*: cleft 100%; single lateral penicillate setules at M0.6 on each side.

Description of holotype (male "a")

Body (Figure 1): 4 mm. *Urosome*: poorly armed dorsally. *Head*: bearing few slender setae dorsally; rostrum obsolescent; eyes absent. *First antenna* (Figure 1): length 0.6x body, 2.4x A2; flagellum longer than peduncle; peduncular article 3 shortest, article 1 longest, ratio of lengths = 22:18:9; setae sparse; flagellum of 18 articles; aesthetascs present on articles 3–15; calceoli absent; accessory flagellum 2 articulate, reaching M0.6 of article 1 of primary flagellum, article 2 tiny; articles of primary flagellum sub-uniform, sparsely setulate. *Second antenna* (Figure 1): length 0.25x body; peduncle much longer than flagellum, article 4 longer than 5, 3–5 with weak ventral setation; flagellum 4 articulate, the apical article bearing a small aesthetasc. *Upper lip*: margin not excavate. *Mandibles* (Figure 1): left mandibular palp 2 articulate, short,

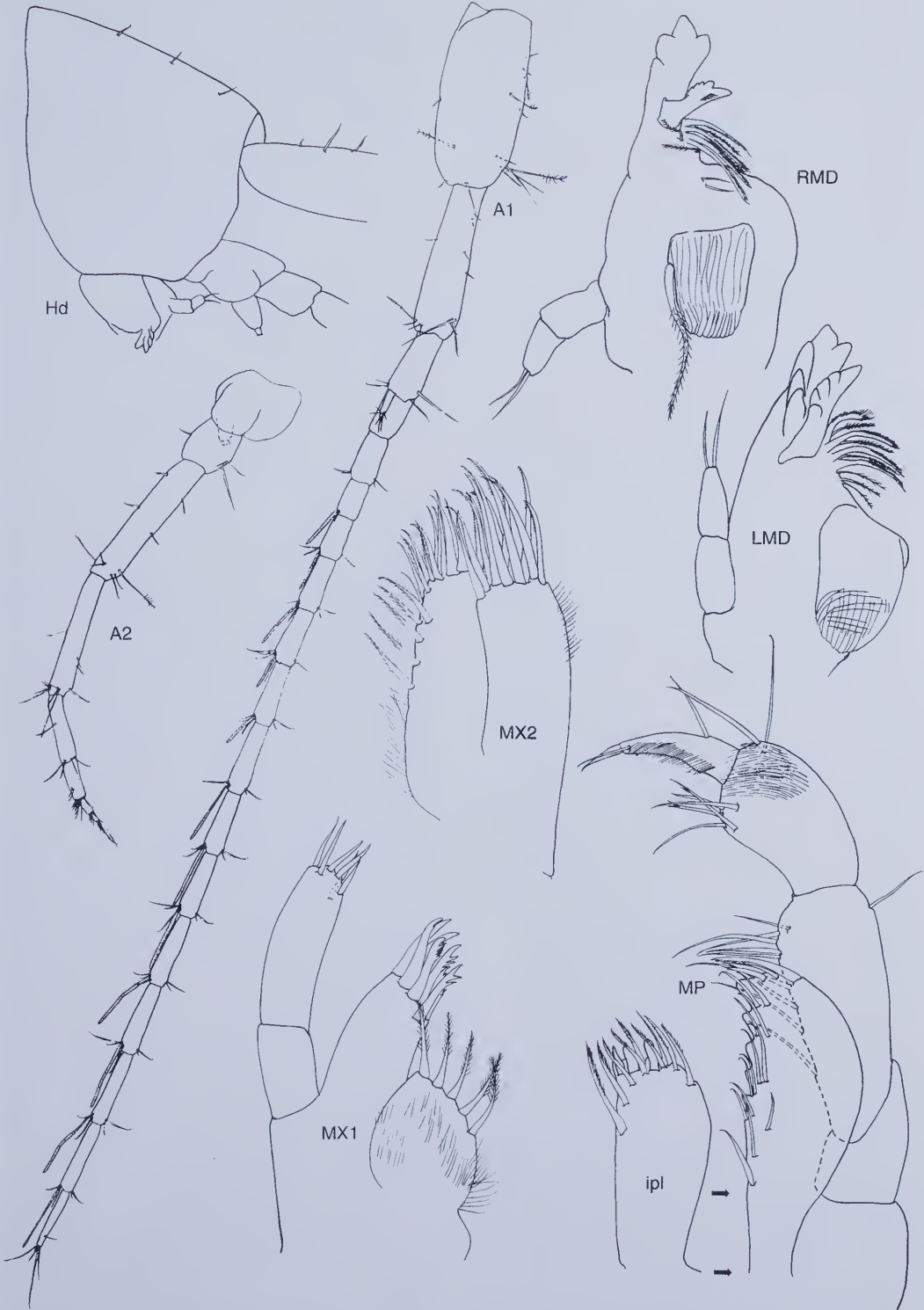


Figure 1 *Nedsia chevronia* sp. nov. Holotype, male 'a' 4 mm. Head, antennae, mandible, maxillae and maxilliped.

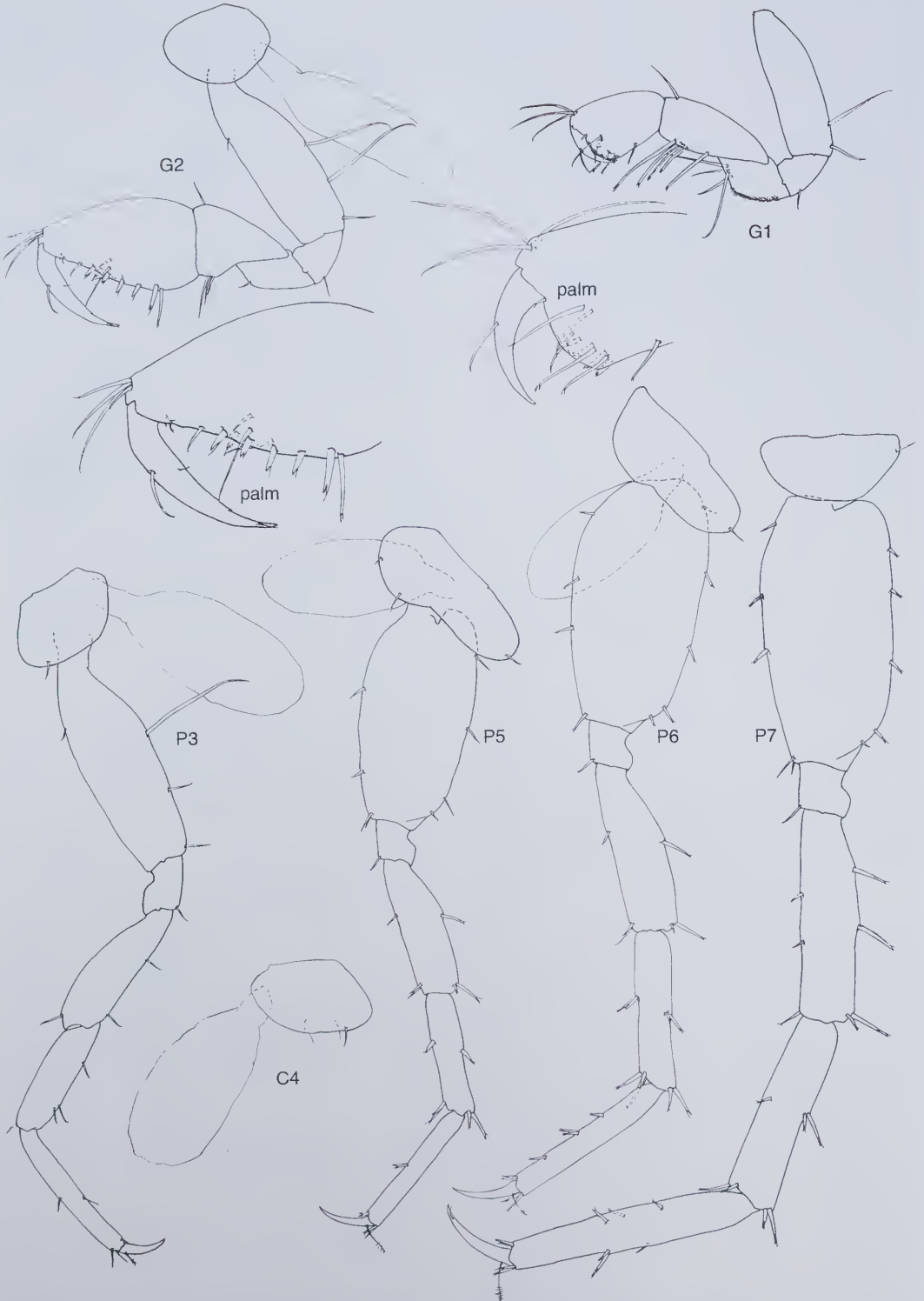


Figure 2 *Nedsia chevronia* sp. nov. Holotype, male 'a' 4 mm. Gnathopods, gnathopodal palms, pereopods 3, 5-7.

articles equal in length, article 2 with 2 long apical E setae; incisor 5 toothed; lacinia mobilis with 5 denticles; 4 setose accessory blades and plumose inter-raker setae; molar without distal plumose seta, triturate, a few small setae basal to the molar; right mandibular incisor 4 toothed; lacinia mobilis barely bifid, broad, finely denticulate anteriorly; accessory blades of 4 plumose setae with few inter-raker plumose setae; molar triturate, bearing a long distal plumose seta; palp 2 articulate, articles of approximately equal length, the distal article tapering, bearing 2 E setae. *First maxilla* (Figure 1): palp article 2 with 6 thin apical setae, all naked; outer plate with 7 denticulate setae; inner plate bearing 5 medio-distal to terminal plumose setae, medial margin and face pubescent. *Second maxilla* (Figure 1): outer plate disto-laterally pubescent; inner plate pubescent on baso-medial margin, bearing medio-marginal to disto-facial row of 5 plumose setae. *Maxilliped* (Figure 1): nail of palp moderately long, dactyl bearing also accessory distal seta as long as the nail, facially bearing fine setae, apex of article 3 not produced, with few thin setae basal to the dactyl, none proximal; inner plate with a disto-facial row of 4 plumose setae, 3 apical naked tooth setae and 4 rastellate or naked setae; outer plate bearing 5 medio-marginal indentations and a row of 11 terminally hooked long slender setae, mostly arranged in pairs. *First gnathopod* (Figure 2): (coxa plate without anterior setae, naked posteriorly); article 4 slightly bulbous posteriorly, bearing short, fine setae; carpus elongate, not lobate; propodus trapezoidal, expanding slightly apically, longer than wide, the posterior edge naked, corner of palm rounded, bearing 2 long, naked lateral setae, and a row of 4 stout bifid setae medially as well as a long slender naked seta, palm slightly convex, dactyl reaching to the palmar corner. *Second gnathopod* (Figure 2): coxa bearing no setae, carpus subtriangular, short; propodus ovate, elongate, naked dorsally, the palmar corner with no medial and 2 lateral setae – one long, slender, apically bifid, the other robust and apically bifid; marginally 4 other stout trigger setae, a single slender seta and small seta basal to the dactyl as well as a long naked slender sub-marginal seta along the lateral palm; medial palm bearing a single robust trigger seta, 2 sub-marginal long slender setae and small seta basal to the dactyl. *Pereopods* (Figure 2): coxa 3 with a single anterior seta; coxa 4 bearing single anterior and posterior setae; P3–(4) longer than G2; P3–5 approximately equal, articles 4,5 sparsely setose posteriorly, propodi of P3–4 bearing single locking setae; P6–7 longer; P5–7 similar but consecutively elongate, each with 2 locking setae; P7 anterior setae of article 6 displaced inward by keel-like expansion of the segment; coxae 5–7 bearing 1,1,1 setae on posterior lobes and 2,0,0 anterior setae; article 2 weakly expanded, greatest on P6, of P7 longest,

none lobate, but extended posteriorly, bearing few setae; dactyls of P3–7 simple, naked except for an anterior basal penicillate setule, with the addition of an outer terminal seta accessory to the nail on P7. *Gills*: coxae 2–6 with flask shaped gills, gill of C3 largest, of C5–6 slightly reduced. *Pleopods* (Figure 3): retinaculæ 2 per pleopod, no accessory retinaculæ; peduncles without apico-lateral setae; rami extending equally, the inner with 5:5:4 articles, the outer with 6:6:6; a single bifid seta on the inner basal articles. *Epimera* (Figure 3): epimera 1–2 postero-ventrally rounded, of E3 sub-quadrate; posterior margin of E1 sinuous, of E2 straight, of E3 barely convex, all smooth, with no setae except a single seta each marking the postero-ventral corner; E2–3 with 1 and 3 ventral setae, lacking lateral oblique ridge. *Pleon* (Figure 3): pleonites 1–6 with few dorso-lateral posterior setae; pleonite 6 with 1 dorso-lateral seta, but without any disto-ventral spinule. *Uropods* (Figure 3): uropod lengths relative to U1 are $U2=0.6x$, $U3=1.6x$; U1 peduncle length $1.5x$ inner ramus, the outer margin bearing a pair of apico-distal setae and reduced row of 2 mid-dorsal setae, the medial apex bearing 2 setae, the medial margin with 2 setae; rami of sub-equal length, both naked except for a single medial mid-dorsal seta on the inner ramus; both rami with 4 terminal setae; U2 peduncle length $0.9x$ inner ramus, bearing 2 apico-lateral and apico-medial setae; inner ramus length $1.5x$ outer, the medial margin bearing 2 setae only, 5 terminal setae; outer ramus shorter, bearing a single mid-lateral seta and 4 apical setae; U3 strongly extended beyond uropods 1–2 in entire animal; peduncle length $0.5x$ outer ramus, shorter than urosomite 3, bearing single mid-dorsal and paired latero-distal marginal setae; outer ramus proximal article with few marginal setae, 4 apico-medial setae, 2 apico-lateral setae and 2 dorsal setae; article 2 shorter ($0.9x$), similarly armed but bearing fine short distal setules medially and laterally, terminating in a cluster of 6 slender setae; inner ramus scale like, sub-quadrate, length $0.14x$ outer, bearing a single apico-medial seta. *Telson* (Figure 3): length $1.3x$ width, widest at base, sub-equal in length to urosomite 3, cleft 100%; apices slightly notched laterally; sub-apices with a long plumose seta, 1 sub-distal medial seta and 1 lateral seta at M0.8, no other dorsal setae except for single penicillate setules on both lobes laterally at M0.6.

Description of other material

Specimen 'b', male: length 3.5 mm. *Pleonite 6* with a single dorso-lateral seta posteriorly. *First antenna*: flagellum of 11 articles, aesthetascs present on articles 5,7,9,10. *Mandibles*: setae of terminal article = 2E; interraker plumose setae present between accessory blades. *Maxilliped*: palp article 3 with 6 slender setae basal to dactyl; nail of dactyl moderately long, bearing 2 slender

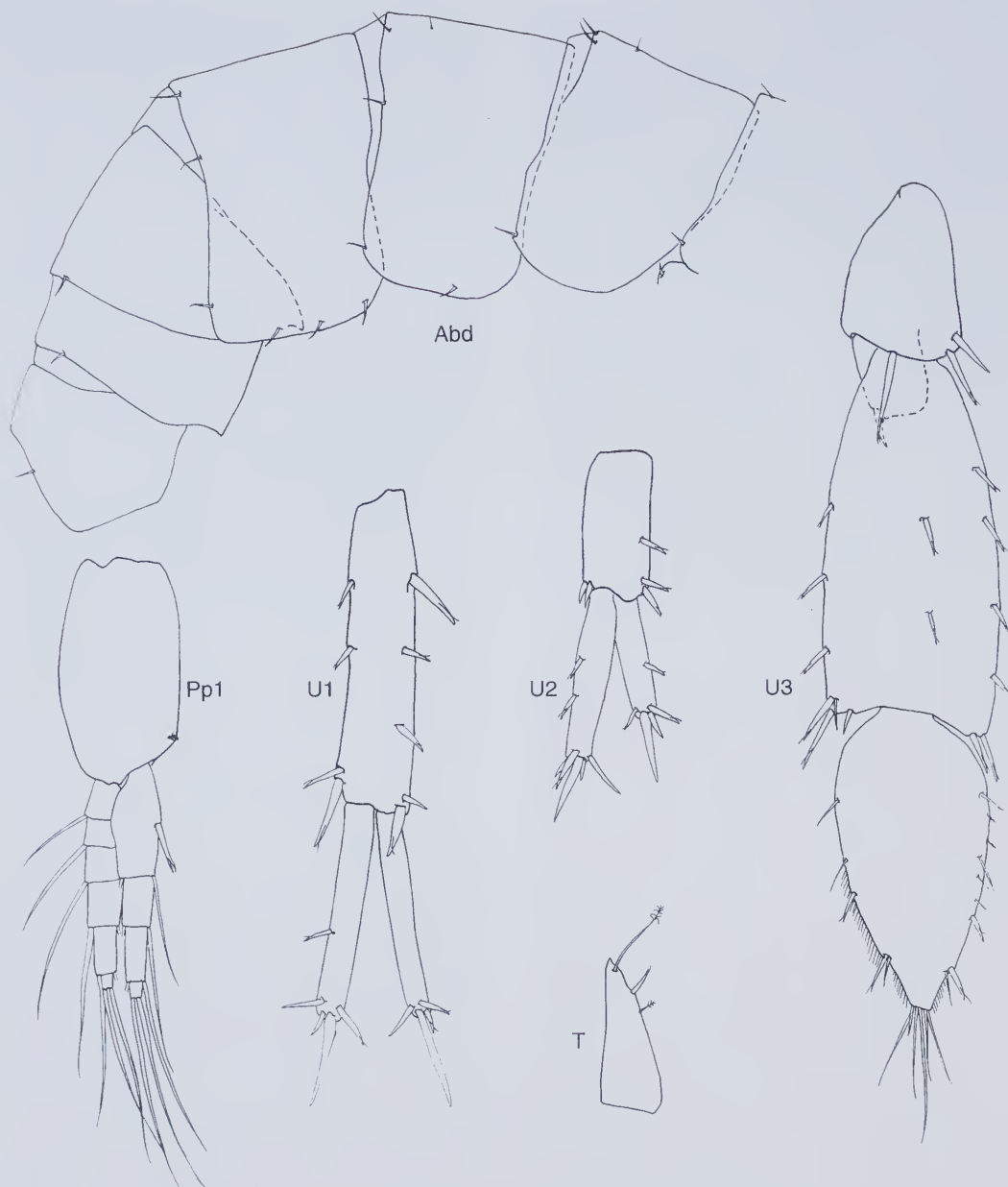


Figure 3 *Nedsia chevronia* sp. nov. All illustrations holotype, male 'a' 4 mm., except where indicated. Abdomen, pleopod 1, uropods and telson. Female allotype 'b' 4 mm. telson.

accessory nails extending slightly beyond the nail. Coxae 1–3 bearing single apical and facial posterior setae; coxa 4 without anterior seta, with facial posterior seta, coxa 5 with single anterior and posterior setae, coxae 6–7 bearing single posterior setae only. Pleopods: accessory setae absent; inner rami of 4:4:4 articles, outer rami of

5:4:4 articles. Uropod: lengths relative to U1; U2 0.6x, U3 1.6x; peduncle of U1 1.1x length of inner ramus, of U2 0.7x; U2 inner ramus 2x outer; peduncle of U3 0.28x length of outer ramus, second article of outer ramus equal in length to first; inner ramus 0.1x outer. Telson: bearing single slender plumose setae subapically.

Distribution

Underground water, MW15/SB36 (field collection number BES3424), bore adjacent the tank farm, Barrow Island oilfields, altitude 9.0 m AHD, on coastal flats, 65 m from coastal cliffs, depth to water surface 9.0 m, the limestone cavernous immediately above and below the water table.

Barrow Island, Western Australia, 20°46'58"S, 115°27'53"E.

Sympatric with *N. hurlberti*: WAM; BES3395, 22 October 1998 (Table 1).

Etymology

Named for Chevron Australia Pty. Ltd., whose assistance enabled this study to be initiated.

Relationships

This species differs from all others of the genus in: the flagellum of the first antenna is of 15 articles; propodus of the first gnathopod bears 2 long, apically bifid slender setae adjacent the corner and 1 short seta basal to the dactyl laterally, and 4 stout robust apically bifid setae from the palmar corner to the mid palm laterally; the propodus of the second gnathopod bears 1 long slender apically bifid and 1 stout robust trigger seta adjacent the palmar corner as well as a row of 4 robust trigger setae and 3 slender setae along the palm laterally, without medial setae adjacent the palmar corner, but 2 long slender and 1 short robust trigger setae midway along the palm as well as a short slender seta basal to the dactyl. The second coxal plate lacks anterior setae; articles 5–6 of the seventh pereopod without a keel like expansion thus anterior setae not displaced inward; rami of pleopods 1–3 of 5,5,4 medial and 6,6,6 lateral articles.

The species also differs from others of the genus by: first antenna peduncle article 1 longest, unlike *N. macrosculptilis* and *N. sculptilis*, and aesthetascs are present on the flagellum whereas in *N. humphreysi* and *N. urifimbriata* they are absent; article 4 of the peduncle of the second antenna is longer than article 5, thus differing from all species except *N. fragilis* and the flagellum is 4 articles long, unlike *N. urifimbriata*, *N. macrosculptilis* and *N. sculptilis*. The second article of the mandibular palp lacks D setae, unlike *N. straskraba*; the incisor bears 5 teeth unlike *N. hurlberti* and the left lacinia bears 5 denticles unlike *N. straskraba*, *N. hurlberti* and *N. humphreysi*; the mandible bears 4 setose accessory blades, differing from *N. halletti*, *N. straskraba*, *N. humphreysi*, *N. fragilis*, *N. macrosculptilis* and *N. sculptilis* and, unlike *N. sculptilis* and *N. fragilis*, bears no other pubescence. The palp of the first maxilla bears 6 slender setae apically similar only to *N. urifimbriata*, *N. hurlberti* and *N. sculptilis*, and the inner plate bears 5 disto-medial plumose setae, unlike all but *N. halletti*; the outer plate of the second maxilla pubescent, unlike *N. stefania*, *N.*

straskraba, *N. humphreysi* and *N. fragilis*. Coxa 2 without posterior setae, unlike *N. straskraba*, *N. fragilis* and *N. macrosculptilis*; coxa 3 with 2 anterior setae, differing from *N. halletti*, *N. stefania*, *N. hurlberti* and *N. macrosculptilis*, and no posterior setae, unlike *N. straskraba*, *N. humphreysi* and *N. fragilis*; coxa 4 bears 1 anterior seta and no posterior setae, thus differing from *N. macrosculptilis*, *N. sculptilis*, *N. hurlberti*, *N. humphreysi* and *N. urifimbriata*. Pereopods 5–7: coxae with 1 posterior seta, differing from *N. stefania* and *N. straskraba*, articles 2 weakly expanded progressively, unlike *N. stefania*, and propodi bear paired locking setae, unlike *N. straskraba*. Pleopods without accessory retinaculae, unlike *N. straskraba*; epimera postero-ventrally rounded, differing from *N. sculptilis*, *N. straskraba*, *N. hurlberti*, *N. urifimbriata*, *N. fragilis* and *N. macrosculptilis*. First and second uropod rami with 4 apical setae unlike *N. halletti*, *N. stefania*, *N. straskraba*, *N. fragilis*, *N. hurlberti* and *N. humphreysi*; third uropod peduncle relatively longer than in *N. fragilis* and *N. macrosculptilis*, and bearing a single mid dorsal seta unlike *N. halletti*, and 2 laterodistal marginal setae and 1 sub apical lateral seta unlike *N. straskraba* and *N. urifimbriata*; the outer ramus proximal article bearing 4 apico-medial and 2 apico-lateral setae and the second article terminates in a cluster of 6 setae, unlike *N. halletti*, *N. straskraba*, *N. urifimbriata* and *N. macrosculptilis*; inner ramus bearing a single apico-medial seta, differing from *N. halletti*, *N. urifimbriata* and *N. macrosculptilis*. The telson relatively longer than all but *N. sculptilis*; cleft 100% unlike *N. sculptilis*; the lobes without submarginal medial setae, unlike *N. sculptilis*, *N. straskraba*, *N. hurlberti*, *N. urifimbriata* and *N. macrosculptilis*; bearing single lateral penicillate setae at M0.5, more basal than in *N. halletti* and *N. urifimbriata*.

Nedsia stefania sp. nov.

Figures 4–6

Type locality

Underground water in L32J old water well, Barrow Island, Western Australia, 20°48'34"S, 115°22'42"E

Material examined

Holotype

♂, 'a' 4 mm (WAMC 28343) Western Australian Museum field collection number BES 3441, L32J, old water well, 20°48'34"S, 115°22'42"E, 24 October 1998, W.F. Humphreys and S.M. Eberhard.

Paratypes

♂, 'b' 2 mm, 2 other, incomplete specimens (WAMC 28344). Same data as holotype.

Diagnosis

Pleonites with few dorsal setae. *Head*: rostrum obsolescent; lateral cephalic lobes moderately to strongly projecting, very broad; no antennal sinus present; eyes absent. *First antenna*: longer than A2; ratio of peduncular articles 2.5:2.5:1. *Second antenna*: short. *Upper lip*: symmetrical; not excavate below. *Mandible*: 3 accessory blades with interraker plumose setae between each main raker; palp 2 articulate, length ratio of articles 1:1, terminal article tapered, setae 2 E. *Maxillae*: moderately setose medially; inner plate of maxilla 1 with 2 (3) medial setae; inner plate of maxilla 2 with row of medial setae extending onto face apically, other medial setae few. *Maxilliped*: inner plate very long with distal row of 2 plumose setae and 3 blunt naked setae; outer plate large, with 3 distal setae, without a blunt naked tooth seta; medial margin carved into sinuities, spineless; sub-marginal face with pairs of setae; palp articles 2-3 weakly setose laterally, article 2 moderately setose medially, article 3 with setae or comb rows of setae near the base of the dactyl, apex not produced, dactyl unguiform, with moderate length nail. *Gnathopods* 1-2 diverse: first gnathopod some setae simple, some bearing trigger hairs and thus asymmetrically bifid, some apically dentate; setae at corner of palm = lateral 1 long trigger, medial 2 robust bifid and 2 slender simple; setae along palm sparse and simple; second gnathopod defining corner with 2 setae. *Coxae* 1-7: with few posterior setae. *Pleopods*: similar; rami extending sub-equally, basomedial setae of inner rami bifid; retinaculæ 2, no accessory retinaculum present. *Epimera*: postero-ventral tooth of epimera 1-3 absent; posterior margins smooth and sparsely setulose; some bearing facial setae near ventral margin. *Pleon*: ventro-distal seta on urosomite 1 at base of uropod 1 absent. *Uropods*: apico-lateral corner of peduncles on uropods 1-2 with 2 and 1 setae, dorsal margins with few setae; medial margin of uropod 1 with 2 apical setae; rami of uropods 1 and 2 extending sub-equally; uropod 1 with basofacial seta; rami of uropods 1-2 with few setae. *Telson*: longer than broad; cleft 100%; lobes weakly convex laterally, with sub-apical plumose setation; lateral setae present.

Description of holotype (male 'a')

Body (Figure 4): 4 mm. *Urosome*: poorly armed dorsally. *Head*: bearing few dorsal setules, rostrum obsolescent; eyes absent. *First antenna* (Figure 4): length 0.4x body, 1.7x A2; flagellum longer than peduncle; peduncular article 3 shortest, article 1 longest, ratio of lengths = 2.3:2:1, setae sparse; aesthetascs present on articles 5-7; calceoli absent; flagellum of 8 articles; accessory flagellum 2 articulate, reaching M0.7 of article 1 of primary flagellum, article 2 tiny; articles of primary flagellum not uniform, sparsely setulate. *Second*

antenna (Figure 4): length 0.2x body; peduncle much longer than flagellum, article 5 longest, 3-5 with weak ventral setation; flagellum 4 articulate, without calceoli. *Upper lip*: margin not excavate. *Mandibles* (Figure 4): left mandibular palp reduced, 2 articulate, articles sub-equal in length, article 2 with 2 long apical E setae; incisor 6 toothed; lacinia mobilis with 5 denticles; 4 setose accessory blades and inter-raker plumose setae; molar without distal pappose seta, tritulative; no other pubescence; right mandibular incisor 4 toothed; lacinia mobilis bifid, broad, finely denticulate; accessory blades of 3 plumose setae and plumose inter-raker setae; palp 2 articulate, molar tritulative, bearing a long distal pappose seta. *First maxilla* (Figure 4): palp article 2 with 5 thin apical setae, all naked; outer plate with 7 denticulate setae; inner plate bearing 2 apico-medial plumose setae, medial margin naked. *Second maxilla* (Figure 4): outer plate devoid of pubescence; inner plate pubescent on baso-medial margin. *Maxilliped* (Figure 4): nail of palp moderately long, medial margin of article 3 with 5 distal thin setae basal to the dactyl, none proximal; inner plate with a row of 3 medial marginal to facial setae, three naked tooth setae and 5 rastellate or naked setae apically; outer plate medial margin bearing 3 deep and one shallow indentations, a single mid marginal seta and a row of 7 mainly paired long naked apically hooked setae adjacent the indentations. *First gnathopod* (Figure 5): coxal plate with a single short seta apically and none postero-ventrally; article 4 slightly bulbous and setate posteriorly; carpus not lobate, longer than wide; propodus trapezoidal, expanding slightly apically, longer than wide, the posterior edge naked, corner of palm rounded, bearing 1 long, naked, apically bifid lateral seta, 2 stout bifid setae and one slender seta medially, palm slightly convex, dactyl reaching slightly beyond the palmar corner. *Second gnathopod* (Figure 5): coxa bearing a single apical seta; propodus ovate, palmar angle acute, palmar corner bearing 2 lateral setae - one long, slender and apically bifid, the other a robust trigger seta -, the mid palm bearing a single slender seta and short seta basal to the dactyl laterally, and medially a slender and a short robust setae. *Pereopods* (Figure 5): coxa 3 without setae, as long as wide, coxa 4 bearing an anterior seta; P3-4 longer than G2; P3-(5) approximately equal, all articles sparsely setose, propodus with only one locking seta; P(5)-7 similar but consecutively elongate, with (2), 2,2 locking setae; P6 anterior seta of articles 5 and 6 displaced inward by keel-like expansion of the segment; coxae 5-7 bearing 1,0,1 setae on posterior lobes, P6-7 articles 2 weakly expanded, subequally, not lobate; dactyls of P3-7 simple, naked except for an anterior basal penicillate setule, with the addition of an outer terminal setule on P6-7. *Gills*: coxae 2-6 with flask shaped gills. *Pleopods* (Figure 6): retinaculæ 2

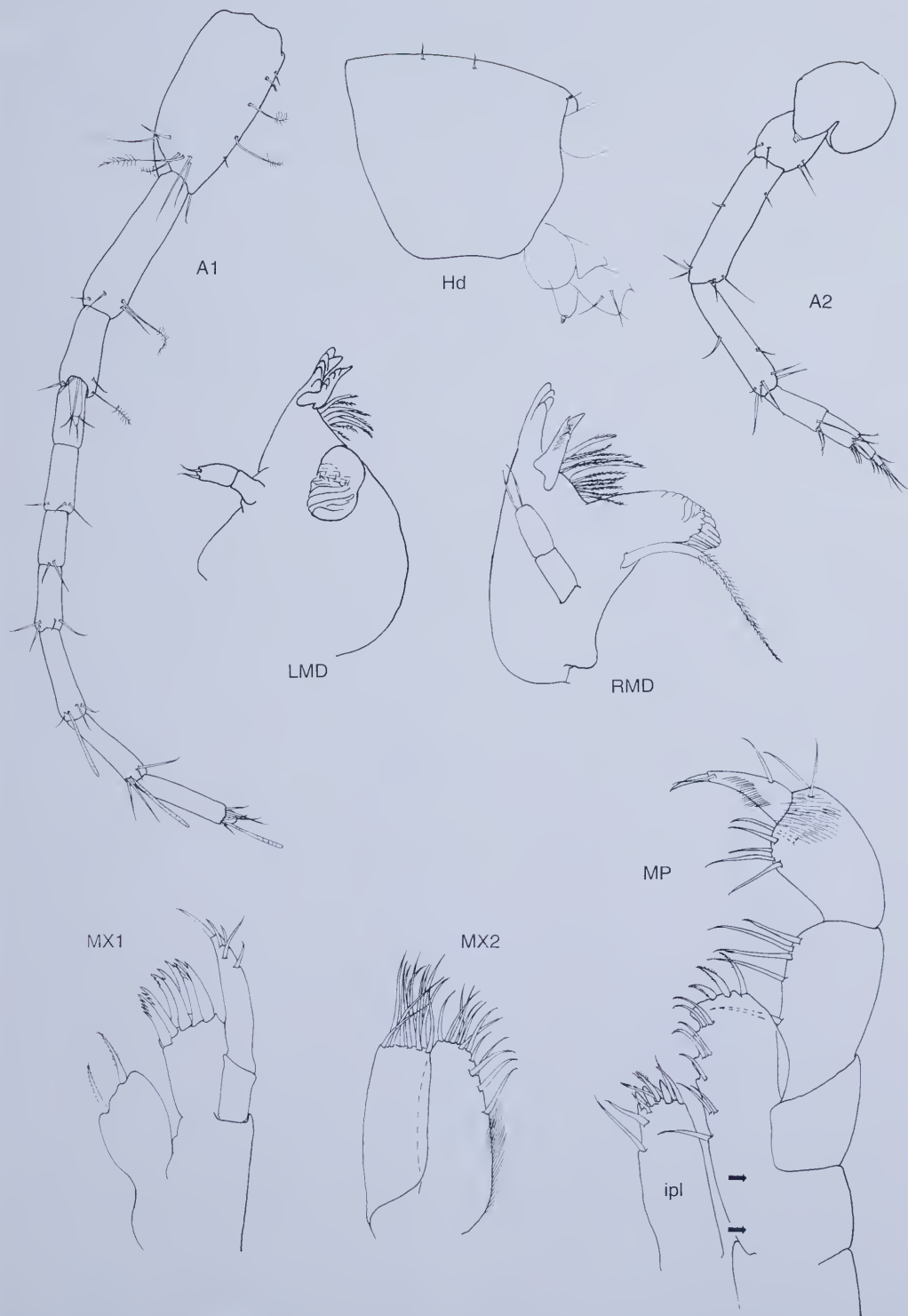


Figure 4 *Nedsia stefania* sp. nov. Holotype, male 4 mm. Head, antennae, mandibles, maxillae and maxilliped.

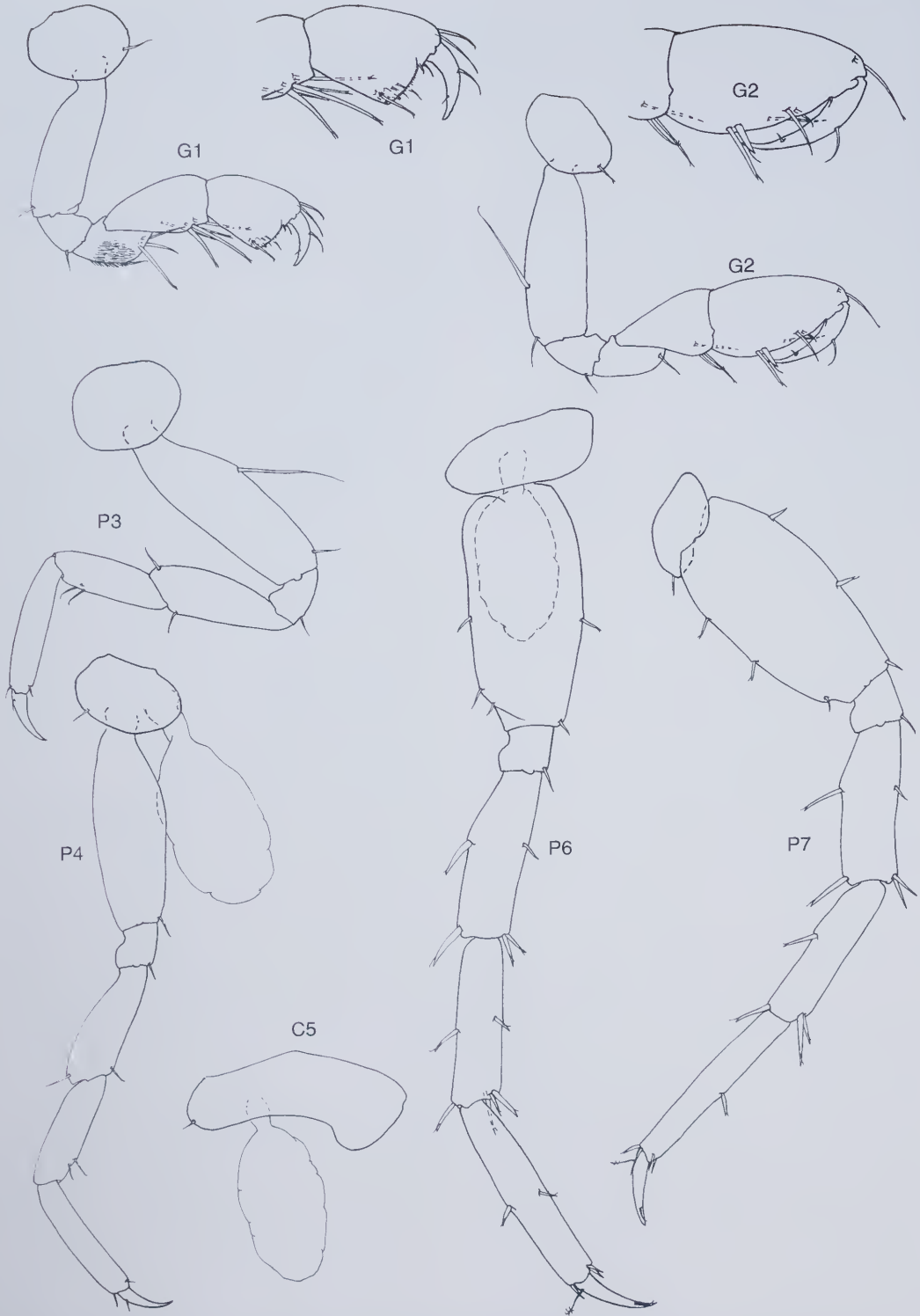


Figure 5 *Nedsia stefania* sp. nov. Holotype, male 4 mm. Gnathopods, gnathopodal palms, coxa 4, pereopods 3, 5-7.

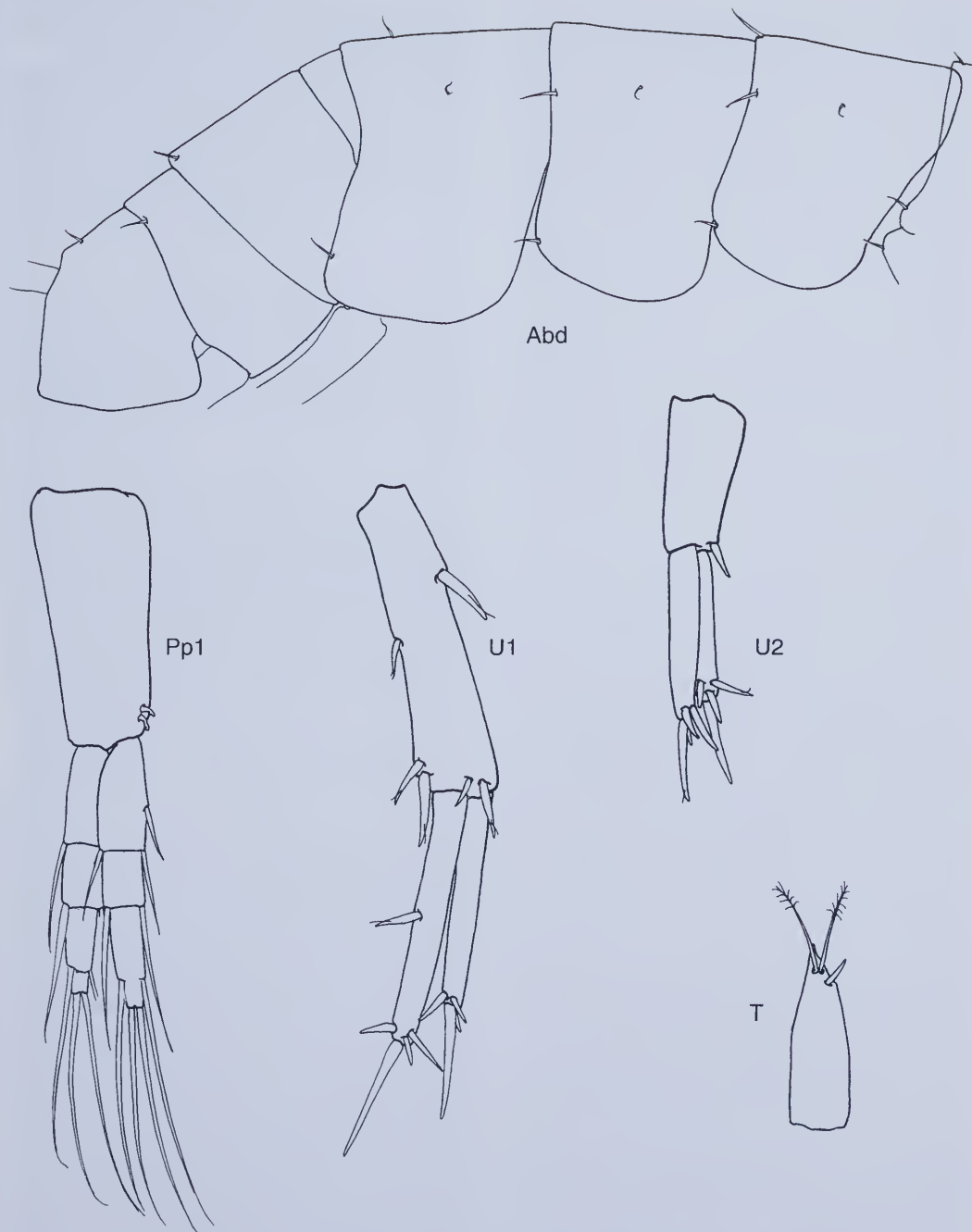


Figure 6 *Nedsia stefania* sp. nov. Holotype, male 4 mm. Abdomen, pleopod 1, uropods and telson.

per pleopod, no accessory retinaculæ; peduncles without other setae; rami extending sub-equally, the inner with 4:4:4 articles, the outer with 4:4:4 articles; no bifid setae on basal articles. *Epimera* (Figure 6):

epimera postero-ventrally rounded; posterior margins scarcely convex on 1-2, slightly concave on E3, all smooth, with few or no setae; ventral setae lacking, each with a single, slender postero-ventral

seta marking the posterior corner. *Pleon* (Figure 6): pleonites 1, 3 and 6 bearing dorsal setae, 1, 2, 4 and 5 with dorso-lateral posterior setae. *Uropods* (Figure 6): length of U2 relative to U1 = 0.6x; U1 peduncle length 1.2x inner ramus, the outer margin bearing two apico-distal setae and no mid-dorsal setae, the medial apex bearing 2 setae, the medial margin bearing a single short robust seta; rami of sub-equal length (inner : outer = 62:52), both naked except for a single mid-dorsal seta on the inner ramus; both rami with 4 terminal setae; U2 peduncle length 0.8x inner ramus, bearing a single apico-lateral seta only; inner ramus length 1.2x outer, the medial margin without setae, 4 terminal setae; outer ramus shorter, also devoid of any but 4 terminal setae; (U3 strongly extended beyond uropods 1–2 in entire animal; inner ramus scale like, sub-quadrate). *Telson* (Figure 6): length 1.5x width, widest at base, sub-equal in length to urosomite 3, cleft 100%; apices slightly notched laterally; sub-apices with 2 long plumose setae, 1 sub-marginal disto-medial seta.

Description of other material

Specimen 'b', male: length 2 mm. *Pleonite* 6: without a dorso-lateral seta. *First antenna*: flagellum (broken), aesthetascs present on articles 3,5. *Mandibles*: ratio of length of palp articles 1–2 = 5:4; setae of terminal article = 2E; interraker plumose setae present between accessory blades. *Maxilliped*: palp article 3 with rows of setae basal to dactyl; nail of dactyl short. *First gnathopod*: coxal plate with single anterior seta and facial posterior seta. *Pleopods*: accessory setae absent. *Uropods*: lengths relative to U1; U2 0.6x, peduncle of U1 1.3x length of inner ramus, of U2 0.8x inner ramus; U2 inner ramus 1.3x outer. Telson bearing a single subapical seta on either lobe.

Distribution

Underground water in L32J old water well (field collection BES3441); disused, steel cased water bore at altitude 50 m above AHD, in the central heights, Barrow Island, ground-water 2 m deep at about sea level.

Barrow Island, Western Australia, 20°48'34"S, 115°22'42"E

Etymology

Named for Stefan Fritz, who facilitated collecting visits to Barrow Island.

Relationships

This species differs from all others in that: the flagellum of the first antenna is of 8 articles; right mandible bears 3 accessory blades; the first maxilla inner plate bears 2 setae medially. The first gnathopod propodus palm bears a single long lateral trigger seta at the corner and only one other

lateral seta basal to the dactyl; the medial corner of the palm bears 2 robust apically bifid and 2 slender simple setae and the palm only one other seta basal to the dactyl. The second gnathopod propodus lateral corner is marked by a long slender trigger seta, and the lateral palm bears 1 mid-marginal slender seta and a small seta basal to the dactyl; medial palm bearing 2 slender simple setae mid way along the palm. Pereopod 2 coxa without an anterior seta. Telson lacking lateral penicillate setules.

Other differences: lacking serration of the pleon and the first article of the first antennal peduncle the longest, unlike *N. macrosculptilis* and *N. sculptilis*; first antenna bearing aesthetascs, unlike *N. humphreysi* and *N. urifimbriata*; the first two articles of the flagellum of the first antenna not fused as in *N. sculptilis* and *N. macrosculptilis*; the second antenna flagellum of 4 articles, unlike *N. urifimbriata*, *N. macrosculptilis* and *N. sculptilis*; mandibular palp without D setae as in *N. straskraba*, the incisor bearing 5 teeth unlike *N. hurlberti* and *N. macrosculptilis* and the mandible bearing 4 setose accessory blades, similar only to *N. urifimbriata*, *N. douglasi* and *N. hurlberti*, the mandible lacking other pubescence, unlike *N. sculptilis* and *N. fragilis*; the palp of the first maxilla bearing 5 slender apical setae, unlike *N. sculptilis*, *N. macrosculptilis* and *N. hurlberti*; the outer plate of the second maxilla devoid of pubescence, differing from *N. hurlberti*, *N. urifimbriata*, *N. macrosculptilis*, *N. sculptilis* and *N. halletti*. First gnathopod coxa bearing 2 anterior and no posterior setae, similar only to *N. halletti*, *N. chevronia* and *N. humphreysi*; coxa of the second gnathopod bearing 2 anterior and no posterior setae, unlike *N. straskraba*, *N. hurlberti*, *N. fragilis*, *N. macrosculptilis* and *N. douglasi*. Pereopods 3–4 subequal in length unlike *N. sculptilis*; pereopods 5 and 7 with paired locking setae, not single as in *N. straskraba*, and coxae 5–7 bearing 1,0,1 posterior setae unlike *N. halletti* and *N. straskraba*, the second articles weakly expanding progressively posteriorly unlike *N. halletti* and not extending posteriorly unlike *N. straskraba*. Pleopods without accessory retinaculae, differing from *N. humphreysi* and *N. straskraba*; both rami of 4,4,4 articles, unlike all except *N. halletti* and *N. fragilis*. Uropod 1 peduncle bearing a reduced row of mid dorsal seta and the medial apex bearing 2 setae, differing from all other species; the rami subequal in length unlike *N. fragilis* and *N. sculptilis*; bearing a single mid dorsal seta medially unlike *N. hurlberti* and *N. urifimbriata*; both rami bearing 4 apical setae, differing from all but *N. halletti*, *N. chevronia*, *N. fragilis* and *N. humphreysi*. The second uropod peduncle approximately equal in length to the inner ramus, unlike *N. halletti*, *N. chevronia*, *N. urifimbriata*, *N. fragilis* and *N. macrosculptilis*; bearing a single apico-lateral seta unlike *N. sculptilis* and *N. hurlberti*; the

inner ramus medial margin naked unlike *N. halletti*, *N. chevronia*, *N. sculptilis*, *N. straskraba*, *N. hurlberti* and *N. urifimbriata*; both rami bearing 4 apical setae, unlike *N. chevronia*, *N. straskraba* and *N. hurlberti*. The telson shorter than *N. halletti*, *N. macrosculptilis* and *N. humphreysi*; cleft 100%, unlike *N. sculptilis*; and lacking submarginal medial setae, differing from *N. sculptilis*, *N. straskraba*, *N. hurlberti*, *N. urifimbriata* and *N. macrosculptilis*.

Nedsia halletti sp. nov.

Figures 7–10

Type locality

Underground water in L32J old water well, Barrow Island, Western Australia, 20°48'34"S, 115°22'42"E

Material examined

Holotype

♂, 'a' 4 mm (WAMC 28345) Western Australian Museum field collection number BES 3462, L32J, old water well, 20°48'34"S, 115°22'42"E, 25 October 1998, W.F. Humphreys and S.M. Eberhard.

Allotype

♂, 'b', 4 mm (28346). Same data as holotype.

Paratype

♂, 'c', 3 mm (WAMC 28347). Same data as holotype.

Diagnosis

Pleonites: with few dorsal setae. *Head*: rostrum weak; lateral cephalic lobes moderately projecting, very broad; no antennal sinus present; eyes absent. *First antenna*: elongate, longer than A2; ratio of peduncular articles 6:5:2; accessory flagellum 2 articulate. *Second antenna*: very short; flagellum much shorter than peduncle; calceoli absent. *Upper lip*: symmetrical. *Lower lip*: with inner lobes. *Mandibles*: accessory blades (rakers) very few (6) on right with interraker plumose setae between each main raker; both mandibles with no additional serrations beyond rakers; mandibular palp reduced, 2 articulate; ratio of articles 1:1, article 1 not setose, terminal article linear, sub-truncate, apical setae 2 E. *Maxillae*: well setose medially; inner plates of maxillae 1–2 poorly covered with pubescence; inner plate of maxilla 1 ovate with 5 medial setae, outer plate with denticulate setae, palps symmetric, with thin apical setae; both plates of second maxilla with apical setae of medium length; inner plate with row of medial setae extending onto face apically, other medial setae absent, medial and lateral margins poorly covered with pubescence.

Maxilliped: inner plate very long with distal row of several setae and 3 blunt naked setae, and short medial row of plumose setae; outer plate large, with few distal plumose setae, continuous without a blunt naked tooth seta; medial margin carved into sinuosities, spineless; sub-marginal face with pairs of setae; palp articles 2–3 weakly setose laterally, article 2 moderately setose medially, article 3 with setae or comb rows of setae near the base of the dactyl, apex weakly produced, dactyl unguiform, with moderate length nail. *Coxae* 1–7: short, broader than long, with few posterior setae; coxa 1 not expanded below; coxa 4 not excavate posteriorly; coxa 5 as long as 4. *Pereopods*: 3–4 of proportions similar to pereopods 5–7; posterior seta sets on article 6 of pereopods 3–4 unevenly spaced. *Pleopods*: similar; peduncles with few setae each; rami extending equally, basomedial setae of inner rami bifid; retinaculæ 2, no accessory retinaculum present. *Gnathopods*: 1–2 diverse; dactyls lacking inner tooth seta, lacking nail. *First gnathopod*: small, feeble, without rastellate seta of article 4; carpus longer than propodus, not lobate; merus lacking hyaline lobe; palm transverse, setae simple, some bearing trigger hairs and thus asymmetrically bifid, some apically dentate; setae at corner of palm = lateral 2 long apically bifid, medial 2–5 short, robust, apically bifid; setae along palm sparse and simple. *Second gnathopod*: weakly enlarged, carpus short and lobate, propodus of medium enlargement and ovate; palm oblique, irregularly spinose and sparsely setose, defining corner with 1 lateral long apically bifid seta. 1 medial robust apically bifid seta. *Pereopods* 5–7: moderately elongate; article 2 moderately expanded, ovato-rectangular, postero-ventrally extended but not lobate; dactyls of pereopods 3–7 lacking accessory spinules. *Gills*: coxae 2–6 each with flask-shaped gill; coxal gill 6 not reduced. *Epimera*: postero-ventral tooth of epimera 1–3 absent; posterior margins smooth, and sparsely setulose; E2–3 bearing facial setae near ventral margin. *Urosome*: ventro-distal seta on urosomite 1 at base of uropod 1 absent. *Uropods*: apico-lateral corner of peduncles on uropods 1–2 with 2 and 2 setae; dorsal margins with setae; medial margin of uropod 1 with 2 apical setae, rami extending sub-equally; outer ramus of uropod 2 shortened; uropod 1 with basofacial seta; most rami of uropods 1–2 with single seta rows; medial setae of outer ramus of uropod 3 sparse, without sub-distal peduncular setae; uropod 3 strongly extended, parviramous, peduncle short, outer ramus 2 articulate, huge; inner ramus scale like, reaching to M0.25 on article 1 of outer ramus. *Telson*: longer than broad; cleft 90–100%; lobes weakly convex laterally, with sub-apical setation; setae, where present, lateral; single lateral penicillate setules at M0.6 to M0.7 on each side.

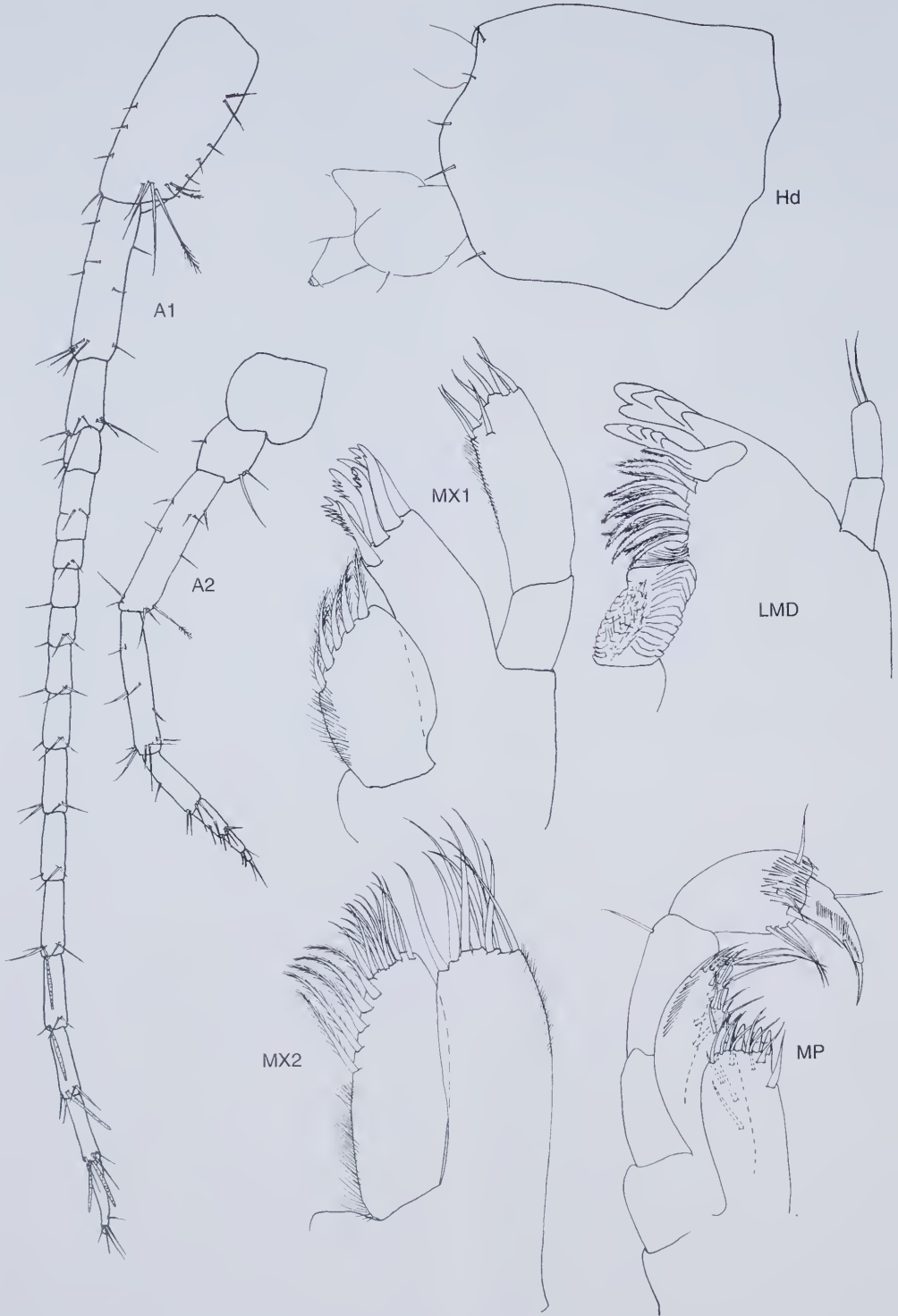


Figure 7 *Nedsia halletti* sp. nov. Holotype, male 4 mm. Head, antennae, mandibles, maxillae and maxilliped.

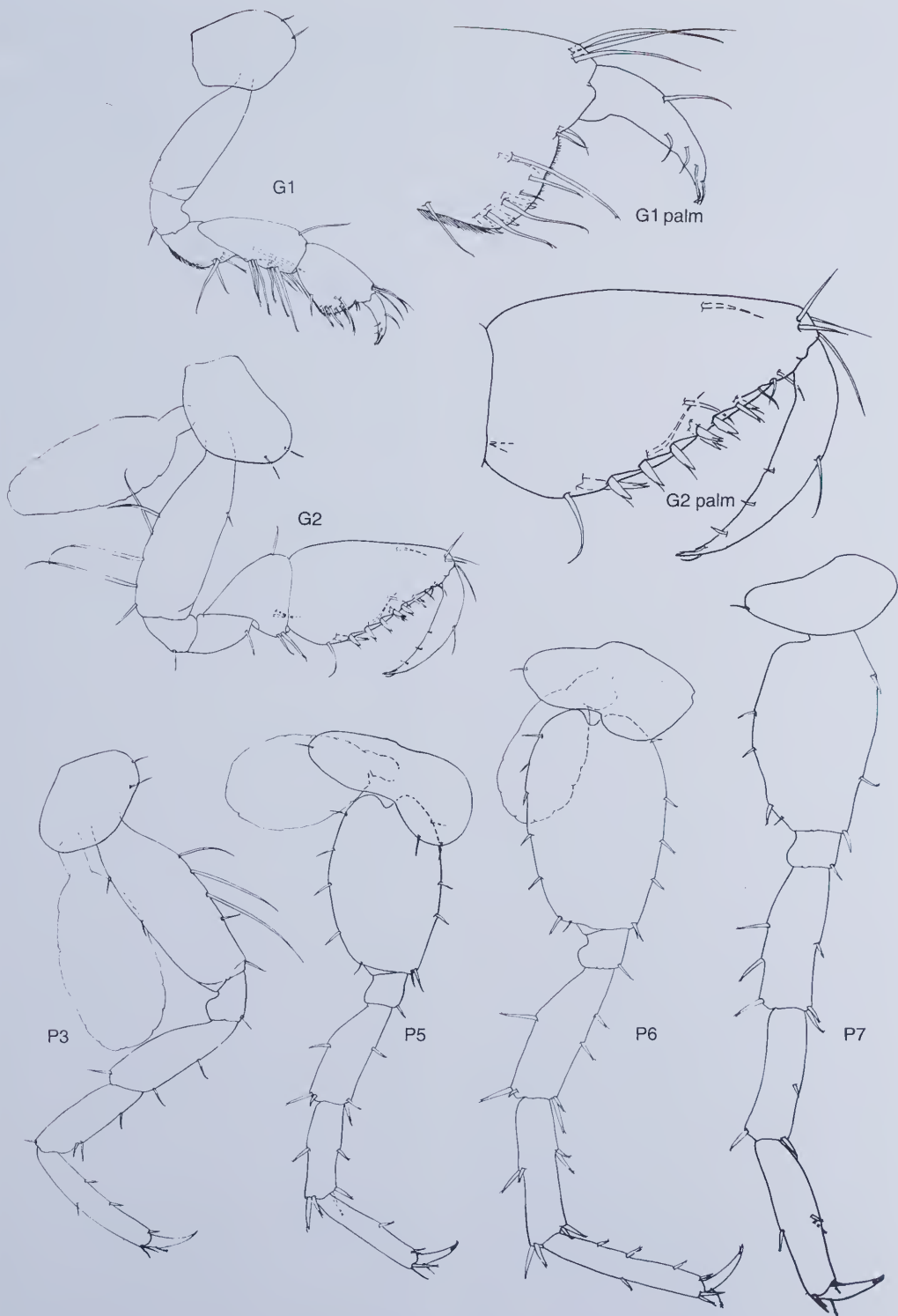


Figure 8 *Nedsia halletti* sp. nov. Holotype, male 4 mm. Gnathopods, gnathopodal palms, coxa 5, pereopods 3,4,6,7.

Description of holotype (male "a")

Body (Figure 7): 4 mm. **Urosome**: poorly armed dorsally. **Head**: rostrum obsolescent; antennal sinus absent; eyes absent. **First antenna** (Figure 7): length 0.4x body, 1.5x A2; flagellum longer than peduncle (1.8x); peduncular article 3 shortest, article 1 longest, ratio of lengths = 62:48:20; setae sparse; flagellum of 16 articles; aesthetascs present on articles 11–14; calceoli absent; accessory flagellum 2 articulate, reaching M0.9 of article 1 of primary flagellum, article 2 tiny; articles of primary flagellum not uniform, but progressively longer, sparsely setulate. **Second antenna** (Figure 7): length 0.25x body; peduncle much longer than flagellum, articles 4–5 equally long (45:42), articles 3–5 with weak ventral setation, lacking robust setae; flagellum short (0.4x peduncle), 4 articulate, no calceoli. **Upper lip**: margin not excavate. **Mandibles** (Figure 7): left mandibular palp 2 articulate, articles sub-equal in length, article 2 with 2 long apical setae (E2) only; incisor 5 toothed; lacinia mobilis with 5 denticles, bearing a postero-facial rugose seta; 6 setose accessory blades; molar without distal plumose seta, tritritative; cluster of fine setae between accessory blades and base of molar; (right mandibular incisor 5 toothed; lacinia mobilis bifid, broad, finely denticulate; accessory blades of 6 plumose spines; palp 2 articulate). **Lower lip**: bearing distinct inner lobes. **First maxilla** (Figure 7): palp article 2 with 6 thin apical and one disto-facial setae, all naked; outer plate bearing 7 denticulate setae; inner plate ovate, bearing 5 apico-medial plumose setae, baso-medial margin pubescent. **Second maxilla** (Figure 7): outer plate bearing pubescence apico-laterally; inner plate pubescent on baso-medial margin, bearing a row of 5 medial marginal tending disto-facial plumose setae. **Maxilliped** (Figure 7): nail of palp moderately long (0.3 of dactyl), palp article 3 with few thin setae at dactylar base, none proximal, apex slightly extended and facially pubescent; outer plate medial margin bearing 4 scallop like indentations distally, a medio-facial row of strong naked setae, 3 apico-lateral naked setae and disto-facial pubescence laterally: inner plate without ventro-facial seta or short spur, with a pair of sub-marginal medial plumose setae apico-facially, three naked tooth setae apically and 4 thin naked apical long setae. **First gnathopod** (Figure 8): coxal plate with two short setae apically and none postero-ventrally; article 4 pubescent and slightly bulbous posteriorly; carpus not lobate, longer than wide; propodus trapezoidal, expanding slightly apically, longer than wide, the posterior edge bearing a single slender seta at M0.6; corner of palm rounded, bearing 2 long, naked, apically bifid setae laterally and 3 stout bifid setae medially, palm slightly convex, bearing few long slender setae; dactyl reaching to the palmar corner. **Second gnathopod** (Figure 8): coxa bearing 2 anterior setae

only; palmar corner marked laterally by a single long slender seta, medially by 1 long, robust trigger seta; palm bearing 5 robust and one slender trigger setae and 2 short slender simple setae adjacent the dactylar base laterally, a single mid-palmar robust trigger seta, 2 sub-marginal slender setae and 1 small seta basal to the dactyl medially; dactyl bearing 3 small sub-marginal setae distally. **Pereopods** (Figure 8): coxa 3 with 2 anterior setae, similar to coxa 1, P3 longer than G2; P3–5 approximately equal, articles 4,5 sparsely setose posteriorly, with only one locking seta; P5–7 similar but consecutively elongate, each with paired locking setae distal on article 6; P7 anterior setae of articles 5 and 6 displaced inward by keel-like expansion of the segment; coxae 5–7 bearing 1,1,1 setae on posterior lobes, 2,0,0 anterior setae, article 2 weakly expanded, most on P7, not lobate, but extended posteriorly and bearing few setae; dactyls of P3–7 simple, naked except for an anterior basal penicillate setule, with the addition of an outer terminal setule on P5–7. **Gills**: coxae 2–6 with flask shaped gills, gill of C3 largest. **Pleopods** (Figure 10): retinaculae 2 per pleopod, no accessory retinaculae; peduncles each bearing 2 apical setae; rami extending equally, the inner with 5:5:5 articles, the outer with 7:6:6; no bifid setae on basal articles. **Epimera** (Figure 10): E1–2 postero-ventrally rounded, E3 sub-quadrate; posterior margins scarcely convex on 1–2, straight on E3, all smooth, with no setae except a single seta marking the posterior corner; E2–3 with 1 and 2 weak sub-marginal ventral setae, lacking lateral oblique ridge. **Pleon** (Figure 10): pleonites 2–5 with dorso-lateral posterior setae; pleonite 6 with 1 lateral and 1 disto-ventral setae. **Uropods** (Figure 10): uropod lengths relative to U1 are $U2=0.6X$, $U3=1.5X$; basal face of U1 bearing a robust seta; peduncle length 1.4x inner ramus, the outer margin bearing 2 apico-distal setae and a row of 3 mid-dorsal setae, the medial apex bearing 2 setae and the medial margin bearing 3 setae; rami of sub-equal length (inner : outer = 92:85), both naked except for a single mid-dorsal seta medial on the inner ramus and lateral on the outer ramus; both rami with 5 terminal setae; U2 peduncle length 0.8x inner ramus, bearing a single apico-lateral seta and 2 marginal setae; inner ramus length 1.2x outer, the medial margin bearing 2 setae only, with 4 terminal setae; outer ramus shorter, bearing a single marginal seta and 4 terminal setae; U3 strongly extended beyond uropods 1–2 in entire animal; peduncle length 0.3x outer ramus, shorter than urosomite 3, bearing paired latero-distal marginal setae and 1 lateral seta, 1 apico-medial seta, and 1 small mid-medial sub-marginal, facial seta; outer ramus proximal article with few marginal setae, some paired, laterally pubescent, and 2 apico-lateral setae; medially 3 apical setae, 3 marginal setae; 2 apical setae basal to the second

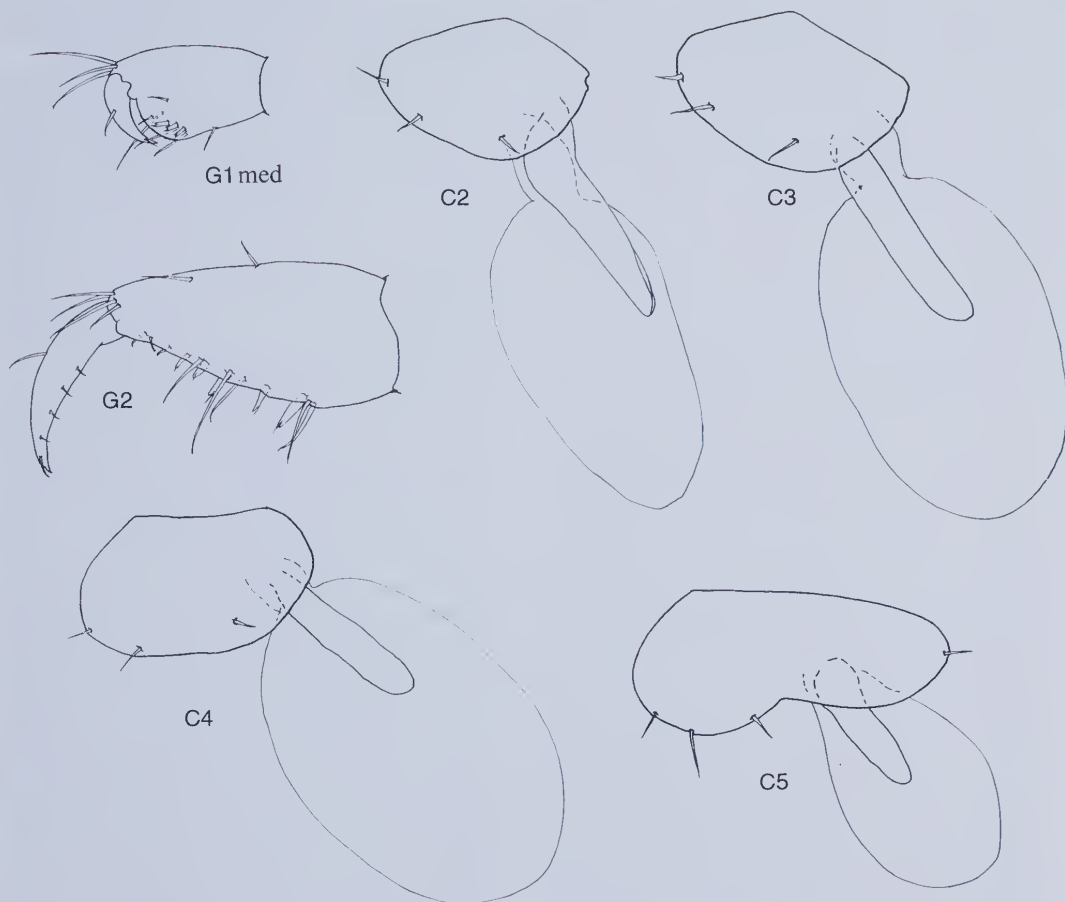


Figure 9 *Nedsia halletti* sp. nov. Allotype, female 'b' 4 mm. Gnathopodal propodi, coxae 2-5 showing coxal gills and oostegites.

article; article two equal in length to the first, similarly armed, lacking pubescence, terminating in a cluster of 8 mixed robust and slender setae; inner ramus scale like, sub-quadrate, length $0.13\times$ outer ramus, bearing paired apico-medial setae. *Telson* (Figure 10): length $1.8\times$ width, widest at the base, sub-equal in length to urosomite 3, cleft 100%; apices slightly notched laterally; sub-apices with 2 long plumose setae, 1 right and 2 left sub-marginal medial setae at M0.7 and 1 lateral seta at M0.5; no other dorsal setae.

Description of allotype (female 'b')

Body: length 4 mm. *Pleonite* 6 bearing single dorso-lateral setae. *First antenna*: aesthetascs absent. *Second antenna*: length of peduncle $4 = 0.9\times$ peduncle 5; flagellum length less ($0.7\times$) than peduncle. *First gnathopod* (Figure 9): propodus small, trapezoidal, expanding apically, $0.6\times$ G2, bearing three long slender lateral setae, and 3 robust apically bifid

setae medially, with few other setae; coxal plate bearing two anterior and one facial postero-ventral setae. *Second gnathopod* (Figure 9): propodus large, ovate, palm acute, marked at corner by an elongate slender seta laterally and one long, slender and one robust apically bifid setae medially; palm bearing additionally two long slender and one short setae laterally, and four robust apically bifid, one long slender and two short setae medially; coxal plate similar to G1. Coxae of pereopods G2 to P6 each bearing a single flask shaped gill, and coxae 2-5 additionally bearing a narrow, strap like, naked oostegite. *Pleopods*: bearing 2 retinaculae, without accessory retinaculae; pleopodal inner rami of 6,6,5 articles, outer rami of 7,6,6 articles. *Uropod*: first uropod length relative to U2 = $1.7\times$; peduncle of U1 $1.3\times$ length of inner ramus, of U2 $0.8\times$ length of inner ramus; *Telson*: (Figure 10): longer than wide; ventral face with a single seta medial sub-marginal at M0.77; length $2.2\times$ width; lateral margin bearing

three setae at M0.3, M0.6, M0.8; dorsal sub-apices bearing a pair of elongate penicillate setae.

Description of paratype (male 'c')

Body length 3 mm. *First antenna*: length 0.5x body, much longer than A2; peduncle shorter than flagellum, flagellum of 16 articles, bearing aesthetascs on articles 10–15. *Second antenna*: peduncle article 4 shorter than article 5 (0.8x), longer than flagellum (3x); flagellum of 4 articles. *Mandible*: palp short, two articulate, articles sub-equal in length. *Gnathopods* and *Pereopods*: similar to type (male 'a'). *Pleopods*: peduncles each bearing 2 retinaculae and no accessory retinaculae; inner rami of 5,5,4 articles, outer rami of 6,6,5 articles. *Epimera*: epimera 1–2 postero-ventral corners rounded, the posterior margins slightly convex; epimeron 3 postero-ventrally sub-quadrate posterior margin straight; each postero-ventral corner marked by a small seta, each posterior margin naked; epimeron 1 without ventero-facial setae, epimera 2–3 bearing 2 and 4 ventero-facial setae, respectively. *Pleon*: pleonites 1–3 each bearing 2 distal setae dorsally and 1 disto-lateral seta; pleonite 4 bearing 2 small dorso-distal setae, pleonite 5 single small dorso-lateral setae and pleonite 6 single dorso-lateral and disto-ventral setae. *Uropods*: uropod 1 length relative to uropod 2 = 1.8x. *Uropod 1*: peduncle bearing a strong baso-facial seta, peduncle length 1.2x inner ramus, bearing 2 dorso-medial and dorso-lateral setae as well as 2 apico-medial and apico-lateral setae; inner ramus bearing only 4 apical setae; outer ramus bearing a single dorso-lateral seta and 4 apical setae. *Uropod 2*: peduncle 0.75x length of inner ramus, bearing 1 dorso-medial and 4 apical setae; inner ramus longer than outer ramus (1.2x), bearing a single dorso-medial seta and 4 apical setae; outer ramus bearing 2 dorso-lateral setae and 5 apical setae. *Telson*: similar to the holotype (male 'a').

Distribution

Underground water in L32J old water well (field collection BES3441); disused, steel cased water bore at altitude 50 m above AHD, in the central heights, Barrow Island, ground-water 2 m deep at about sea level.

Barrow Island, Western Australia, 20°48'34"S, 115°22'42"E.

Etymology

Named for Keith Hallett who generously imparted of his knowledge of the ground water environment of Barrow Island.

Relationships

N. halletti differs from all other described species of the genus *Nedsia* in: primary flagellum of the

first antenna of 16 articles; mandibles bear 7 setose accessory blades; the palm of the first gnathopod bears 2 long naked lateral setae adjacent the corner and 3 other long setae along the palm, and 3 stout bifid setae medially as well as a single slender seta basal to the dactyl; the second gnathopodal corner is marked by a single slender seta laterally and a long robust trigger seta medially, the palm bearing 5 robust and 1 slender trigger setae as well as 2 slender setae basal to the dactyl laterally and single robust and slender trigger setae as well as 3 other slender setae medially; the uropodal rami bear 5:5:5 medial articles and 7:6:6 lateral articles; the second article of the outer ramus of the third uropod is as long as the first, and bears 7 terminal setae.

As well as the above universal differences, *N. halletti* differs from *N. macrosculptilis* and *N. sculptilis* in lacking posterior serration of the pleon, in the elongate first rather than the second article of the first antennal peduncle, and the non-fused first two articles of the primary flagellum; *N. halletti* differs from *N. macrosculptilis*, *N. sculptilis*, *N. urifimbriata* and *N. douglasi* in that the primary flagellum of the first antenna bears aesthetascs; the second antenna flagellum is 4 articulate rather than 5; the mandibular palp is of 2 equally short articles unlike *N. straskraba*, *N. hurlberti*, *N. urifimbriata*, *N. fragilis* and *N. douglasi* in which the first article is shorter than the second; the second article of the mandibular palp bears 2 only E setae unlike *N. straskraba* which also bears 2 D setae; the incisor is 5 toothed compared with 4 in *N. hurlberti*, and the left lacinia mobilis bears 5 denticles and the mandible pubescent, unlike *N. hurlberti*, *N. straskraba* and *N. humphreysi* which each have 4 denticles and also, along with *N. urifimbriata*, lack mandibular pubescence. The palp of the first maxilla bears 7 apical setae, unlike all other *Nedsia* spp. except *N. hurlberti*; the outer plate of the second maxilla is pubescent, thus differing from *N. straskraba*, *N. humphreysi*, *N. fragilis* and *N. stefania*, as well as on the inner plate, unlike *N. humphreysi* and *N. fragilis*. The first coxal plate bears 2 apical setae, unlike *N. hurlberti*, *N. humphreysi* and *N. fragilis* and *N. douglasi*, and is without posterior setae whereas *N. straskraba*, *N. urifimbriata* and *N. fragilis* each bear 1, and *N. douglasi* two; the second coxa is similar to the first and different from *N. straskraba*, *N. fragilis*, *N. macrosculptilis* and *N. douglasi*, although *N. hurlberti* bears no posterior setae on the second coxa; coxa 3 differs from all except *N. sculptilis*. The lengths of pereopods 3–4 are approximately equal, unlike *N. sculptilis*; P5–7 bear paired locking setae, not single on P5 and P7 as in *N. straskraba* and the second articles are approximately equal, not progressively expanded, as in *N. straskraba*, *N. hurlberti* and *N. humphreysi*. Pleopods bear no accessory retinaculae as do *N. straskraba* and *N. douglasi*; the first epimeron is without ventro-facial

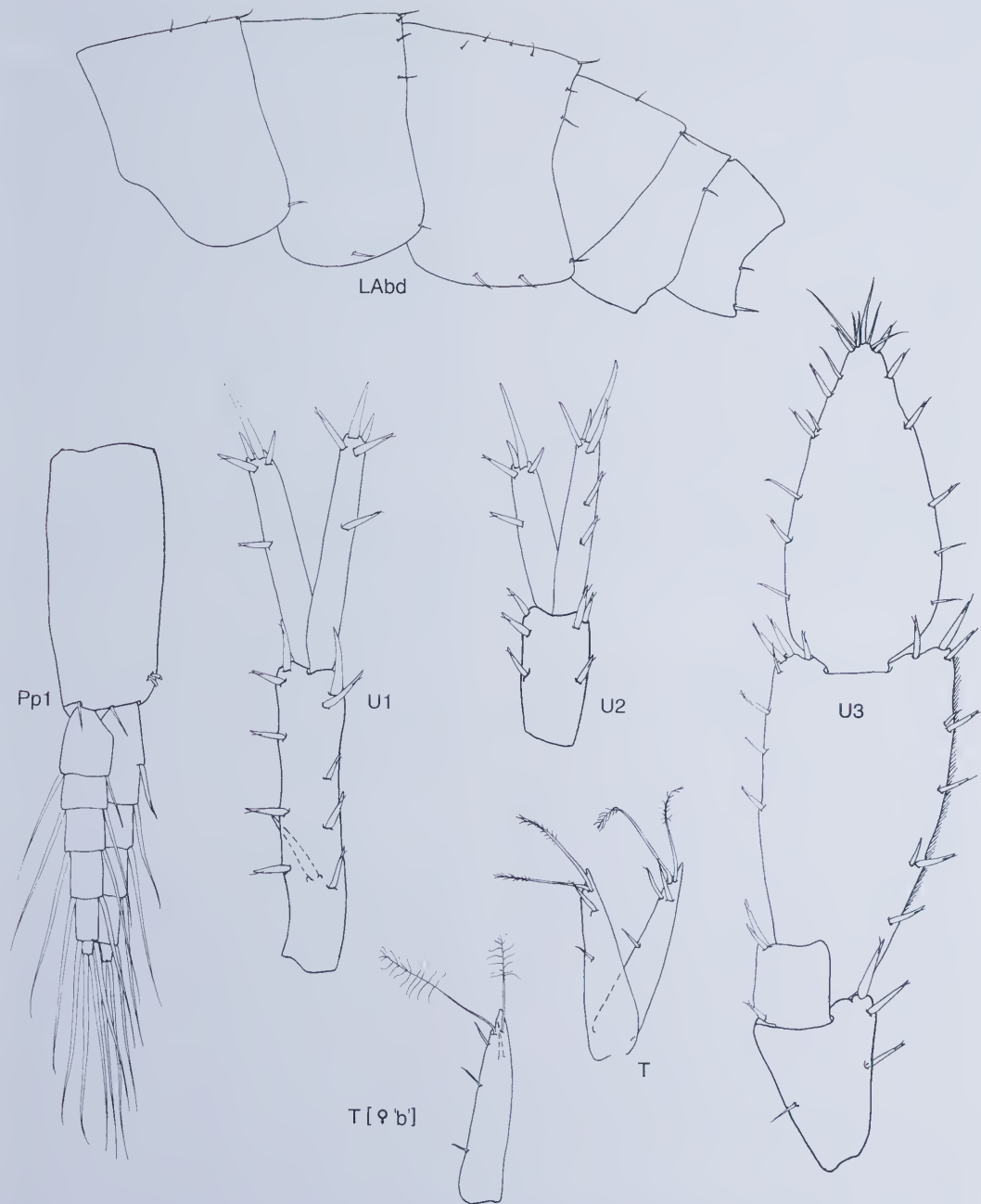


Figure 10 *Nedsia halletti* sp. nov. Holotype, male 4 mm. Abdomen, pleopod 1, uropods 1–2 and telson.

setae unlike *N. douglasi*, which bears 1; the second epimeron bears a single ventral seta, unlike all other species except *N. chevronia*, and the third epimeron 2 ventral setae, similar only to *N. straskraba*; pleonites 4–5 bear single dorsolateral posterior setae, differing from all but *N. urifimbriata*, *N.*

stefania and *N. chevronia*; the peduncle of the first uropod bears 1 apico-distal, 4 mid-dorsal and 1 apico-medial setae similar only to *N. hurlberti*, rami are sub-equal in length, unlike *N. sculptilis* and *N. fragilis*, naked except for a single mid-dorsal seta on the inner ramus rather than paired setae as in *N.*

hurlberti and *N. urifimbriata*, and bearing 4 apical setae similar only to *N. stefania*, *N. chevronia*, *N. fragilis* and *N. humphreysi*, all others bearing 5 apical setae; likewise, the second uropod differs from all other species. The peduncle of the third uropod is proportionally longer than in other species excepting *N. chevronia*, bears paired disto-lateral marginal setae rather than single setae as in *N. straskraba* and *N. urifimbriata*, no sub-apical seta, compared with 3 in *N. urifimbriata* and 1 in *N. straskraba*; the first article of the outer ramus differs, in numbers of marginal setae from *N. douglasi*, in numbers of apical setae from *N. macrosculptilis*, *N. chevronia*, *N. straskraba* and *N. urifimbriata*; and the second article is equal to, not shorter than, the first, unlike all other species, bears 7 terminal setae, more than any other species, and the inner ramus bears paired apico-medial setae, thus differing from *N. straskraba*. Telsonic lobes are more slender than all but *N. humphreysi* and *N. macrosculptilis*, are without dorsal setae as in *N. douglasi*, cleft 100%, unlike *N. straskraba* (85%), and bear single lateral penicillate setules on either lobe at M0.5, more basal than other species excepting *N. urifimbriata*.

Remarks.

The three new species of the genus *Nedsia* described here are derived from samples taken at seven locations on Barrow Island between October 1998 and April 1999 (Appendix 1). The nature of the habitat and methods of collection of these stygobionts, which are small, fragile, and some of the appendages attenuate, are such that complete specimens are difficult to obtain; often, also, the majority are juveniles, and usually few specimens are collected at any one site. Consequently, material from several locations could not be identified with absolute certainty. Nevertheless, much of the material has been assigned to species wherever possible, based upon the presence of gross characters. Thus, for example, *N. sculptilis* or *N. macrosculptilis*, characterised by unique sculpturing of the pleon, were recognised from 5 samplings of 4 locations. Other specimens recorded include *N. straskraba* – 3 samples from one location; *N. humphreysi* – 1 sample (1 site); and *N. hurlberti* – 2 samples from 2 locations.

Barrow Island is one of the few Western Australian marine karst areas studied in any detail (Humphreys, 1993a,b; 1999, 2000), and, like other stygobiont sites in Western Australia where any intensity of sampling has been carried out (Bradbury and Williams, 1997; Bradbury, 2000; Watts and Humphreys, 1999, in press), has proved to be a significant, species rich region. Further sampling may yield more species from the Island: indeed several of the samples examined here

included specimens which could not be reliably identified because of damage or immaturity, yet had the appearance of new, undescribed taxa.

Keys to the first seven of these species of the genus *Nedsia* were set out in Bradbury and Williams (1996a, 1999). From these, *N. chevronia* keys to position 6, then: coxa 1 without setae; telson without dorsal setae; maxillipedal outer plate length 2.4x width. *N. stefania* keys to position 3, then: epimera 1 bearing disto-lateral setae; peduncle of first uropod bearing facial seta; first gnathopod palmar corner rounded; outer plate of maxilliped not apically rounded, medial cusps strong. *N. hallettii* keys to position 6, then: coxa one bearing anterior, but no posterior, setae; telson bearing dorsal setae; maxillipedal outer plate length 2.9x width.

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Appendix 1 Collection number, site details and locations.

WAM #	Site	Collector	Details	Date	No.	Latitude	Longitude
3395	A	WFH/SME	MW15/SB36	22/10/98	17	20°46'58"S	115°27'53"E
3424		WFH/SME	MW15/SB36	23/10/98	5		
3397	B	WFH/SME	MW17	22/10/98	3	22°46'43"	115°28'14"
3407	C	WFH/SME	L8, old water supply well	22/10/98	2	20°49'01"	115°23'40"
3420		WFH/SME	L8, old water supply well	23/10/98	2		
3439		WFH/SME	L8, old water supply well	24/10/98	1		
6969		K.Hallett	L8, old water supply well, mid point	13/01/99	1		
6980		K.Hallett	L8, old water supply well, surface	13/01/99	1		
7301		K.Hallett	L8,old water supply well, surface	15/04/99	1		
7305		K.Hallett	L8, old water supply well, middle	15/04/99	1		
3411	D	WFH/SME	M62, tank supply pump #2, surface	22/10/98	1	20°49'08"	115°24'24"
3431		WFH/SME	M62, tank supply pump #2, surface	23/10/98	1		
6987		K.Hallett	M62, tank supply pump #2, surface	13/01/99	1		
6990		K.Hallett	M62, tank supply pump #2, surface	13/01/99	3		
3441	E	WFH/SME	L32J old water well	24/10/98	8	20°48'34"	115°22'42"
3462		WFH/SME	L32J old water well	25/10/98	3		
6983	F	K.Hallett	L4N, unused anode well, surface	13/01/99	1	20°48'22"	115°23'21"
6984		K.Hallett	L4N, unused anode well, mid point	13/01/99	1		
7308		K.Hallett	L4, bottom sample	16/04/99	1		
7001	G	K.Hallett	M13, new unused anode well, surface	13/01/99	1	20°49'02"	115°24'44"

WFH = W.F.Humphreys; SME = S.M.Eberhard. WAM = Western Australian Museum.

A forgotten scorpion: the identity of *Buthus flavicruris* Rainbow, 1896 (Scorpiones), with notes on *Urodacus manicatus* (Thorell)

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William J. Rainbow (1856–1919), whilst entomologist at the Australian Museum, Sydney, published a series of papers on the arachnid fauna of Australia and nearby regions. By modern standards these papers are generally imperfect but, to his credit, Rainbow illustrated the somatic and genitalic features of many of these species, a custom which was not yet firmly established amongst his contemporary arachnologists. One of these papers (Rainbow, 1896) contained the description of a new species of scorpion, *Buthus flavicruris* Rainbow, based upon a specimen collected from Cooma, New South Wales. This species was not cited by Koch (1977) or Fet *et al.* (2000), and appears to have been completely overlooked since the publication of the paper. The specimen cannot be found amongst the collections of the Australian Museum, Sydney (Mr G. Milledge, pers. comm.), and is considered lost.

Rainbow's (1896) figures, although somewhat rudimentary, clearly demonstrate that the species is not a member of the genus *Buthus*, or even of the Buthidae, but of a species of *Urodacus* (Urodacidae). The only *Urodacus* species found in that part of south-eastern Australia is *U. manicatus* (Thorell), which was redescribed and illustrated by Koch (1977). The description and illustrations of *B. flavicruris* match those of *U. manicatus* moderately well, although Rainbow's (1896) illustration of the metasoma of *B. flavicruris* (Rainbow, 1896, figure 4a) shows slightly more strongly developed dorsal keels than those of *U. manicatus* illustrated by Koch (1977). This discrepancy is probably due to Rainbow's sketchy style of illustration, rather than any real differences within the Cooma population. The dimensions quoted by Rainbow are well within the range of variation found in *U. manicatus*, as is the number of pectinal teeth – 16 – which indicates that Rainbow's specimen was probably a male.

We have no hesitation in placing *B. flavicruris* as a synonym of *U. manicatus* (new synonymy), despite the slight discrepancies between the published illustrations as noted above.

Urodacus manicatus is widespread throughout south-eastern Australia, ranging as far north as

southern Queensland and as far west as the Flinders Ranges, South Australia. Although *U. manicatus* has been recorded twice from Western Australia, we consider these records to be incorrect. Pocock (1891) suggested that the two specimens from Western Australia described by Keyserling (1885) under the name *U. novaehollandiae* Peters were misidentified, and he proposed the name *U. keyserlingii* for the specimens. He later (Pocock, 1893) placed *U. keyserlingii* in the synonymy of *U. abruptus*. If this synonymy is correct, then we doubt the locality given for Keyserling's specimens.

The only other record of *U. manicatus* in Western Australia is that by Harvey (1981) from Madura. However, reexamination of these specimens shows that they represent *U. novaehollandiae*, a species which is commonly found along the southern edge of the Nullarbor Plain (Koch, 1977).

We therefore consider that *U. manicatus* does not occur in Western Australia, and is restricted to south-eastern Australia as depicted by Koch (1977). *Urodacus manicatus* – under the name *U. abruptus* Pocock – has been the subject of ecological and behavioural studies (Smith, 1966; Southcott, 1955), making it one of the better known of all Australian scorpions. It is commonly found on the slopes of the southern highlands of New South Wales and Victoria where it constructs shallow burrows under rocks and, less often, under logs (Smith, 1966). We here provide the primary synonymy of the species, based upon the list provided by Fet *et al.* (2000).

Urodacus manicatus (Thorell)

Ioctonus manicatus Thorell, 1876: 14–15. Type locality: Australia (as "New Holland").

Urodacus abruptus Pocock, 1888: 174–175, figs 4, 4a. Type localities: Adelaide, South Australia; and Australia (as "New Holland").

Urodacus keyserlingii Pocock, 1891: 245. Type locality: Western Australia, but probably incorrect (see above).

Buthus flavicruris Rainbow, 1896: 634. Type locality: Cooma, New South Wales. **New synonymy.**

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***Paramonacanthus oblongus*, the correct name for the Indo-Pacific fish currently called *P. japonicus*, with a recommendation on the nomenclature of *Stephanolepis cirrifer* (Tetraodontiformes, Monacanthidae)**

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Members of the monacanthid genus *Paramonacanthus* Bleeker are small fishes (commonly known as leatherjackets and filefishes) that inhabit flat silty and sandy bottoms throughout the Indo-West Pacific. The genus was recently revised by Hutchins (1997), who recognised 11 species. Among these was *P. japonicus* (Tilesius, 1810) from the eastern Indian and West Pacific Oceans. However, we have since discovered that Tilesius's name is preoccupied and here correct the nomenclature of the species, as well as provide a new recommendation concerning *Stephanolepis cirrifer* (Schlegel, 1850) from Japan and China.

Paramonacanthus japonicus was originally described (as *Balistes japonicus*) by Tilesius (1810) on the basis of a single specimen (presently lost) from Japan (see Hutchins, 1997: 29). However, Tilesius was unaware that *Balistes japonicus* had been used earlier by Walbaum (1792). Walbaum's description is very brief, but is nevertheless sufficient to make the name available:

"Species adhuc dubiae

20. BALISTES, *japonicus*, radiis pinnae dorsalis 3 v. 4. W. Balistes monoceros. *Einhörnliche Hoornvisch*. Houttuyni. Act. Harl. XX. P. 2. n. 33. D. 3-4. P. 13. V ... A... C. 14. Longitudo 6 unciarum. Color subfuscus vel cinereus. Anteriorum radiorum unus exit in longum filum."

This indicates that Walbaum's description was based on the earlier account of Houttuyn (1782) under the name *Balistes monoceros*. Houttuyn's description (p. 345) is reproduced here:

"34. (stated as 33 by Walbaum) BALISTES MONOCEROS. *Eenhoornige Hoornvisch*

Van deezen Visch, die in de beide Indien huisvest, heb ik een schoon groot Exemplaar van Japan ontvangen. Het is meer dan zes Duimen lang, en overtreft dus in groote de Afbeelding van een zodanigen, welke ik volgens een Voorwerp, uit het Kabinet van den Wel Ed. Heer W. VAN DER MEULEN, nu ruim zestien Jaaren geleeden, aan't licht bragt (h). In Kleur niet alleen, die bruin is of graauw, mar ook in de telling der Vinstraalen, komt het daar

mede vry wel overeen: want ik vind in de Rugvin en Aarsvin, beiden, drie of vierendertig, in de Borstvinnen dertien, en in de Staartvin veertien Straalen. Het byzonderste is, dat een der voorsten van de Rugvin uitloopt in een langen Draad."

Our translation of Houttuyn's description is as follows:

"These fish that live in both Indies I have received a good example from Japan. It is more than 6 thumbs long. I compared it with a figure of something similar which was brought to light 16 years ago from the cabinet of Mr W. van der Meulen. It compares well not only in colour which is dull brown but also in the fin rays: the back fin and anal fin both three or four and thirty (= thirty-three or thirty-four), the breast fin thirteen and the tail fin fourteen rays. The most outstanding feature is the first of the back fin which runs in one long thread."

Walbaum's description deviates from Houttuyn's in several features, most notably in recording only 3–4 dorsal rays and not providing a count for the anal fin. We surmise that this may have resulted from confusion over his translation of Houttuyn's phrase: "want ik vind in de Rugvin en Aarsvin, beiden, drie of vierendertig" (see above). Apparently it was also enough to cause subsequent workers to ignore Walbaum's name.

Houttuyn's description appears to have been based on a species belonging to the Monacanthidae. It was, as stated in the introduction to Houttuyn's paper, collected by Carel (= Carl) Thunberg in Japan and provided to Houttuyn through the auspices of J.C.M. Radermacher. The meristic values—allowing for a count of 14 caudal-fin rays which is two more than is typical for the family—and elongate, threadlike filament in the dorsal fin suggest that it was based on *Stephanolepis cirrifer* (Schlegel, 1850). There are no balistids in the Japanese region that possess an elongate ray anteriorly in the soft dorsal fin and the only other Japanese monacanthid so adorned is *Pervagor nigrolineatus* (Herre), a species that occurs in the

Ryukyu Islands (Matsuura and Sunobe, 1990) and possesses only 25–30 anal-fin rays (Hutchins, 1986). Therefore *Balistes japonicus* Walbaum, 1792, is most likely a senior synonym of the species originally described by Schlegel (1850) as *Monacanthus cirrhifer*. However, as mentioned above, we are unaware of the use of Walbaum's name for this or any other species since it was first described. Conversely, *Stephanolepis cirrhifer* has been universally applied to this species in recent literature (see below), and we thus advocate its continued use.

Article 23.9 of the International Code of Zoological Nomenclature requires that the adoption of a younger name over a disused older one must be accompanied by evidence that the younger name has been used as the presumed valid name in at least 25 works, published by at least 10 authors in the immediately preceding 50 years, and spanning at least 10 years. Therefore, the following works are submitted here to fulfil this requirement: Abe (1986), Burgess and Axelrod (1972), Chyung (1961, 1977), FAO (1992), Kamohara (1967), Konishi (1995), Masuda and Allen (1987), Masuda *et al.* (1975, 1984), Masuda and Kobayashi (1994), Matsuura (1979), Murofushi and Yosida (1979), Nakabo (1993), Okada (1955), Patzner and Moosleitner (1999), Randall *et al.* (1997), Safran (1990), Safran and Omori (1990), Shen (1994), Shiino (1972), Sokolovskaya *et al.* (1998), Taguchi (1985), Tyler (1980), and Vasil'yev (1980).

According to Article 57.2 of the International Code of Zoological Nomenclature, *Balistes japonicus* Tilesius (1810) is a junior primary homonym of *Balistes japonicus* Walbaum (1792), and is thus permanently invalid. Hutchins (1997) showed that the next available name for Tilesius's species is *Monacanthus oblongus* Schlegel (1850). Hutchins noted that Schlegel's description is composite, being based on specimens of the present species and *Thamnaconus septentrionalis* (Günther); he also noted that the "type illustration" was based on a male of the present species. However, he was unaware that Boeseman (1947: 209) had also showed that Schlegel's description was a combination of two species, and had in turn designated a lectotype for the species (Boeseman's description of the lectotype [RMNH 4133b] clearly identifies it with a male specimen of the species called *Paramonacanthus japonicus* by Hutchins, 1997). The correct name for this species thus becomes *Paramonacanthus oblongus* (Schlegel, 1850).

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